THESIS

SOIL TEXTURAL CONTROL OVER DECOMPOSITION AND SOIL ORGANIC MATTER DYNAMICS

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY NEAL A. SCOTT ENTITLED SOIL TEXTURAL CONTROL OVER DECOMPOSITION AND SOIL ORGANIC MATTER DYNAMICS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

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ABSTRACT OF THESIS

SOIL TEXTURAL CONTROL OVER DECOMPOSITION

AND SOIL ORGANIC MATTER DYNAMICS

Soil texture is an important factor that influences litter decomposition and soil organic matter (SOM) dynamics, but few experiments have addressed specific mechanisms. Even less work has been done to answer the question of how important abiotic driving variables interact with soil texture to affect decomposition. I used laboratory soil incubations coupled with a simulation model to describe the interaction of soil texture with soil water availability and nutrient availability. I also addressed the importance of litter placement (surface vs. incorporated) across a gradient of texture, moisture and nutrient availability.

The laboratory experiment was a randomized complete block design. Treatments consisted of texture (73%, 55%, 40% sand), water availability (-0.012 MPa, -0.033 MPa and -0.3 MPa), nutrient availability (plus nitrogen (100 mg kg^{-1}) and phosphorus (40 mg kg^{-1}), ambient soil levels), litter placement (surface and incorporated), and replicates (3). Soils were packed into cores at a bulk density of 1.45. Wheat litter (C/N = 19) labeled with ^{14}C was added to the soil cores at a rate approximating 2200 kg ha^{-1}, total C

addition being 2170 mg C kg^{-1}. The cores were incubated for 90 d. Respiration ($^{14}C/^{12}C$-$CO_{2)}$ was measured weekly except during the first 10 d, when it was measured every 5 d.

The fine textured soil lost more $^{14}CO_2$ and $^{12}CO_2$ than either of the other soils when litter was incorporated. Soil water potential significantly affected litter decomposition, the -0.012 MPa treatment decomposing faster than either the -0.033 or -0.3 MPa treatment, both of which were similar. Nutrient addition had no effect on decomposition for either litter placement treatment. Litter placement had no effect on the rate of decomposition. When the respiration data were divided into 3 time periods (0-10, 11-51 and 52-90 d), there was greater loss of surface $^{14}CO_2$ from the coarse soil during 0-10 d (surface litter only). The overall 90 d effect of texture was not significant. Respiration rates correlated significantly to percent water-filled pore space (%WFPS) regardless of litter placement, although incorporated litter showed much less variability than did surface litter. Addition of litter carbon stimulated the mineralization of soil organic C, contributing significantly to the overall respiration rates during the incubation.

Nutrient interactions may play an important role in decomposition and organic matter dynamics, though they appeared unimportant in this experiment. A simulation model was constructed to analyze possible interactions between carbon, nitrogen and phosphorus during decomposition. Percent water-filled pore space controlled the utilization rate of litter C and SOM. Microbial C/N ratio controlled uptake rates of all

C pools. Simulated results using high C/N ratio substrates showed slower decomposition than laboratory data, leading me to suspect that the simulated division of plant C into structural and metabolic C was incorrect. The model provided the opportunity to test ideas about the effect of texture and soil water potential on decomposition and SOM dynamics across a range of abiotic conditions and litter types.

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DEDICATION

This work is dedicated to the memory of my parents, Harriet and Reginald Scott. Without their support and understanding through my youth, I doubt I would be writing this thesis today. To them, I say thank you.

ACKNOWLEDGEMENTS

So many people contributed to the work described in this thesis it is impossible to thank them all. I would like to thank my committee members and my advisor, Vern Cole, for their guidance and advice throughout this project. In particular, I'd like to thank Ted Elliott for his valuable contributions to several aspects of this project. I would also like to thank the other graduate students at the Natural Resource Ecology Lab (notably Cindy Cambardella, Robin Reid, Steve Huffman, John Zachariasen, Alister Metherell) who helped make my Masters' program intellectually challenging and a lot of fun. I would also like to thank all the members of the lab crew at NREL (Dan Reuss, Stephanie Stern, Louise Odeen, Mark Lindquist). Many thanks to Mike Ryan and Dan Binkley for their constructive reviews.

Without the cooperation of Steve Huffman, this research project would never have become a reality. Steve gave the project an important second dimension, providing valuable camaraderie along the way. Thanksgiving eve has a new meaning for me as a result of this project.

Finally, I'd like to thank my wife Chris. She may have borne more of the burden of my Masters program than I. Her support was infallible. I know her wish in life is that some day graduate school will be over. To Chris, thanks so much and hang in there.

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INTRODUCTION

Soil texture is an important control on ecosystem scale patterns and processes. Across the Great Plains, sand content is positively correlated to patterns of primary production (Burke et al. 1990). At the microsite scale, texture may control the establishment of species growing in semi-arid environments such as *Bouteloua gracilis* (Bill Lauenroth personal communication). Some ecosystem models that couple primary production to decomposition and organic matter formation use soil texture to predict rates of organic matter stabilization (Parton et al. 1987). For each of these examples, the control of texture is either direct (a function of the different soil solid particles) or indirect (influencing some other soil physical factor that can regulate microbial activity). Direct effects of texture include changes in soil surface area and chemical properties of clay minerals that influence soil stabilization. Indirectly, texture influences soil water availability, soil nutrient availability and soil temperature. Soil texture control of ecosystem processes is by nature either correlative or mechanistic. When used as a correlative control, the exact mechanism is often not explicitly stated or examined empirically. This work will focus on examining the direct and some indirect effects of soil texture on plant litter decomposition.

Not only does soil texture control decomposition both directly and indirectly, but these different controls may be important at different temporal scales. Soil texture may have no effect on decomposition during the initial rapid decay of plant material, yet may dominate long-term stabilization of plant material into soil organic matter. It is important to specify the time scale over which a control is important. Experiments that study textural effects on decomposition must address direct vs. indirect controls, and also the time scales over which these controls are important.

My objective was to examine some specific effects of soil texture on short-term decomposition of plant residue. The fact that soil texture influences decomposition and SOM dynamics is well documented. When this influence occurs during decomposition is not as well understood. Using laboratory incubations, I empirically ascertained the importance of several controls on decomposition rate. These controls were then be integrated using a simulation model of short-term plant litter decomposition (90 d). The simulation model was used to assess whether the important controls on decomposition (be they direct or indirect) had the same effect across a gradient of litter quality, soil water, soil texture, and nutrient availability.

LITERATURE REVIEW

Decomposition is the critical process that recycles nutrients sequestered in plant biomass. Decomposition is the breakdown of plant material by the soil biota. SOM is an alternate source of C available to soil microorganisms. Mineralization of SOM is the breakdown of organic C formed in the soil during decomposition and other microbial processes (metabolism, death etc.). Like plant litter, SOM is composed of different fractions with different turnover times (Parton et al. 1987). At an ecosystem scale, litter production, decomposition and SOM dynamics are tightly coupled to regulate nutrient availability.

Several factors interact to control rates of decomposition and SOM formation and mineralization. Soil texture is an important physical factor that influences the turnover rate of SOM and the breakdown of plant litter. Texture also influences several other soil physical factors such as water availability and aggregation. Soil texture controls decomposition both directly and indirectly. The processes by which texture regulates decomposition and SOM dynamics may vary through time and across gradients of soil physical factors. It is easy to study the effects of a single soil factor on decomposition, but more difficult to study the interaction of this factor with other biotic and abiotic factors that influence rates of SOM turnover and decomposition.

Factors that regulate decomposition and SOM dynamics

Higher quality plant litter (low lignin/N or low C/N ratio) usually decomposes faster than poorer quality litter under identical physical conditions (Stott et al. 1983; Melillo et al. 1982; McClaugherty et al. 1985; Melillo et al. 1989). Litter incorporated into the soil generally decomposes faster than litter left on the surface. This is important when comparing no-till to conventionally tilled agroecosystems (Brown and Dickey, 1970; Nyhan 1975; Douglas et al. 1980; Holland and Coleman, 1987; Cogle et al. 1987). The presence of live plants has been shown to depress decomposition in some cases (Jenkinson 1977; Martin 1987), possibly by providing an alternate C source to microbes via root exudation. Soil pH is an important control on the rate of decomposition (Alexander 1977). Soils with higher clay content have higher surface area, increasing the number of exchange sites where organic molecules and microorganisms can be stabilized (Ladd et al. 1981; Sorenson 1981; van Veen et al. 1985; Merckx et al. 1985; West et al. 1988). This is the most important direct effect of soil texture on decomposition. Several other factors strongly related to soil texture influence decomposition. Higher soil water availability can elevate rates of decomposition up to some critical level of soil moisture (Bhaumik and Clark, 1947; Floate 1970; Wildung et al. 1975; Sommers et al. 1981; Stott et al. 1986; Doran et al. 1988; Sparling et al. 1989; Summerell and Burgess, 1989). Increased nutrient availability *usually* stimulates decomposition. This is particularly evident with low quality residue (Puig-Giminez and

Chase, 1984; MacKay et al. 1987; McClaugherty et al. 1985). However, nutrient additions have slowed or had no effect on the rate of decomposition in some studies (Fog 1988). Knapp et al. (1983) and Reinertsen et al. (1984) provided evidence that soluble carbon in plant residue controls the rate of decomposition, especially during the early stages of decomposition. Warmer temperatures can stimulate decomposition up to some threshold level (Wildung et al. 1975; Stott et al. 1986).

Indirect effects of soil texture

Water availability

Soil texture controls soil moisture availability and nutrient availability by altering the pore volume and pore size distribution in the soil. Soils have a characteristic bulk density that is a function of particle size distribution. Increased clay content leads to lower bulk density, higher total pore volume and a greater number of smaller pores compared to sandy soils. This strongly regulates water potential (water availability) in the soil. The higher the clay content, the greater the volume of soil water retained in the soil matrix at a given matric potential. Whether this translates to greater water availability is not certain.

Nutrient availability

The maintenance of a particular protoplasmic elemental stoichiometry is a critical concept for many areas of ecosystem research

(Reiners 1986). Potentially mineralizable N and P increase (higher nutrient availability) as organic matter content increases in grassland ecosystems (Schimel et al. 1985; Schimel 1986). Nutrient availability regulates primary productivity, SOM formation/mineralization and decomposition (Chapin et al. 1986; McClaugherty et al. 1985). Soil aggregation is an important factor that can confound the relationship between SOM and nutrient availability. The relationship between soil texture, aggregation and organic matter quality is poorly understood (Christensen and Sorensen, 1985; Cindy Cambardella personal communication). During aggregate construction, organic matter is sequestered into a range of particle size fractions. The breakdown of SOM in these fractions depends not only on organic matter quality but also physical protection of the different size fractions (Tisdall and Oades, 1982; Elliott 1986). Methods are currently being developed to assess SOM quality in different size fractions (Cindy Cambardella personal communication). Eventually, it may be possible to measure the turnover times of different organic matter pools held in different size fractions.

Organism mobility

Movement of soil microinvertebrates through the soil matrix is regulated by pore size distribution. As pore diameter decreases, the mobility of protozoa and other mobile grazers decreases. Small pore diameter can physically isolate microsites from larger invertebrates. These sites provide protection to microorganisms, reducing the rate of nutrient

turnover and SOM formation. Grazers enhance soil nutrient availability by mineralizing microbial biomass. This prevents microbes from becoming a large sink of important nutrients (Anderson et al. 1978; Elliott et al. 1984; Ingham et al. 1986).

Direct effects of soil texture

Soil texture and soil organic carbon content are strongly correlated on a regional scale (Burke et al. 1990). As clay content increases, the surface area of the soil and the number of charged exchange sites increases (Sorenson 1981). This allows for greater stabilization capacity of soluble organics and microbial cells as clay content increases. The effect of clay on stabilization depends to some extent on the clay mineralogy of a soil. For example, kaolinite has a lower capacity to bind protein molecules than does montmorillonite (Marshman and Marshall, 1981a; 1981b). The effect of greater surface area has been used to drive simulation models of decomposition and organic matter formation (Parton et al. 1987). It is important to stress, however, that the basis for using this direct effect of soil texture is correlative in nature. These factors have never been assessed independently of other factors that *may* mediate the direct effect of soil texture.

So how does soil texture control decomposition? Is the direct effect of surface area on C stabilization the most important factor? Or is the indirect effect of texture on soil water potential the primary mechanism responsible

for the influence of texture on SOM dynamics? It is possible that the interaction of two or more factors is the most important influence on decomposition. Do any of these controls become more or less important with changes in soil texture? This experiment attempted to clarify the mechanisms behind textural effects on the rate of litter decomposition across a textural gradient. It also looked at the interaction between physical controls, their variation through time and their interaction with time.

CHAPTER I

MECHANISMS OF SOIL TEXTURAL CONTROL ON THE DECOMPOSITION OF WHEAT LITTER AND THE MINERALIZATION OF SOIL ORGANIC MATTER

INTRODUCTION

Soil texture is an important control on decomposition and soil organic matter (SOM) formation. Simulation models of decomposition and organic matter formation employ soil texture as a key driving variable to control stabilization of soil organic matter (Parton et al. 1987). There is a strong positive correlation between percent sand and soil organic carbon across large regions of the Great Plains in both cultivated and native systems (Burke et al. 1990). Particle-size distribution interacts with other abiotic factors that influence microbial activity and SOM formation. Laboratory decomposition experiments rarely examine the independent effects of soil texture and other abiotic factors as well as their interaction on rates of decomposition and SOM formation in a single experiment.

Particle-size distribution controls SOM dynamics in several ways. The higher the clay content, the greater the surface area and number of exchange sites available to stabilize organic C (Sorenson 1981; van Veen et al. 1985; Merckx et al. 1985). Sand (or silt, clay) content regulates bulk density and pore-size distribution, both of which control the activity of the

soil biota. The volume, size distribution and continuity of soil pores regulate soil water availability, gas diffusion and movement of soil organisms (Elliott et al. 1980; Elliott et al. 1984; Coleman et al. 1984). These soil physical factors also regulate soil water availability. Soil water content (or distribution) affects O_2 permeability, diffusion of fresh substrate to soil organisms and removal of microbial produced biocidal metabolic products. The interaction of these three processes determines the optimum soil water content for peak microbial activity. Up to this threshold soil water content, microbial activity and soil water content are positively correlated. Above this threshold, microbial activity is inhibited by greater soil water content (Bhaumik and Clark, 1947; Sommers et al. 1981; Stott et al. 1986; Sparling et al. 1989; Skopp et al. 1990). The addition of inorganic nutrients may stimulate decomposition, especially when the substrate has a high C/N or lignin/N ratio (Hunt et al. 1989; Puig-Gimenez and Chase, 1984; MacKay et al. 1987; McClaugherty et al. 1985); however, exceptions do occur (Fog 1988). During early stages of decomposition, microbial biomass increases rapidly. Eventually, C may become limiting to microbial growth. This will alter the maximum size of the microbial biomass and therefore the rate of decomposition (Reinertsen et al. 1984; Knapp et al. 1983). There are other soil physical factors controlled by particle-size distribution, but they are not examined in this study. All the factors listed control rates of substrate decomposition and mineralization of native SOM.

The effect that substrate addition may have on native SOM is frequently debated. Many studies have addressed the effect of inorganic N addition on the mineralization of soil organic nitrogen (Jenkinson et al. 1985). This added nitrogen interaction can alter the interpretation of ^{15}N fertilization experiments (Jenkinson et al. 1985). The effect of labile C or plant litter addition on the mineralization of SOM is not clear (Dalenberg and Jager, 1989; Dalenberg and Jager, 1981; Jenkinson 1971). The contribution of native SOM and microbial C to mineralized SOM is difficult to distinguish. This makes it difficult to identify the specific source of respired native SOM. The contribution of native SOM to total respiration during litter decomposition is likely small (Dalenberg and Jager, 1989; Jenkinson 1971). Some experiments show substantial "priming" (stimulated native SOM mineralization following substrate addition), but these results are often attributed to faulty methods such as the use of non-uniformly labeled plant litter (Broadbent and Norman, 1946). No work has examined the importance of soil texture and other related factors on the "priming effect". Soil priming could change the dynamics of decomposition and long-term dynamics of SOM formation.

Carbon-14 respiration can be used to measure the decomposition rate of labeled plant litter (Stott et al. 1986; Puig-Gimenez and Chase, 1984; Reinertsen et al. 1984; Voroney et al. 1989; Shields and Paul 1973; Ladd et al. 1985; Jenkinson 1977; Cogle et al. 1987; Martin 1987). This technique does not directly measure rates of mass loss because litter carbon can be

immobilized into microbial biomass or converted to soil organic matter. Van Veen and Paul (1981) stressed the importance of these biosynthetic reactions on the interpretation of decomposition results. The percent of added ^{14}C remaining through time is the sole measure of decomposition in these experiments. Analysis of other factors such as the distribution of the remaining ^{14}C could provide valuable information about processes controlling SOM formation.

Cogle et al. (1987) compared mass loss of confined (litter bag) and unconfined litter against respiration of ^{14}C from unconfined labeled litter as alternative measures of decomposition. Decomposition rates measured using confined litter were lower than rates measured using mass loss of unconfined litter or ^{14}C loss from labeled litter. When comparing studies that use different measures of decomposition, results should be interpreted considering the method used to measure decomposition. This is especially true when considering biotic controls where no information on the pool size or activity is available (e.g., grazers of microorganisms).

The objective of this study was to examine the importance of particle-size distribution, soil water availability and nutrient availability as controls on decomposition and SOM dynamics. Because particle-size distribution influences soil water availability and nutrient availability, the importance of the interaction of these factors on decomposition and SOM dynamics was assessed. More specifically, I addressed the following hypotheses:

- Litter decomposition is faster in sandier soils because less litter C is stabilized into SOM (this could be stated as a lower "conversion efficiency" for sandier soil).
- When abiotic conditions (soil moisture, nutrient availability) are favorable, surface litter decomposes faster than incorporated litter because surface litter C is respired rather than forming SOM.
- Increased soil matric potential increases rates of decomposition up to some threshold level, above which anaerobic conditions inhibit litter decomposition. Particle-size distribution and soil water matric potential interact to regulate decomposition because soil texture strongly controls soil water availability.
- The factors that control decomposition also regulate SOM mineralization. More native SOM will be lost from the finer textured soil when no substrate is added because the greater the clay content, the larger the pool of SOM.

MATERIALS and METHODS

Soils used in this experiment were taken from the summit and toeslope of a toposequence with uniform land use history in Baca County, Colorado (Wood 1990). The site is currently under cultivation as part of a long-term study on the effects of crop rotation patterns on SOM dynamics. The coarse (summit) and fine (toeslope) textured soils were Ustollic Haplargids and Ustollic Paleargids, respectively (Table 1.1).

Table 1.1. Physical characteristics of 3 soils used in the experiment.

	Soil characteristics			
Texture class	%sand	%silt	%clay	C_{org} (g kg^{-1})
sand	73	20	7	2.8
sandy loam	55	30	15	5.4
loam	40	40	20	8.1

The medium textured soil was a mixture of the coarse and fine soil. Soils were collected at random from the top 20 cm.

Wheat (*Triticum aestivum)* was pulse labelled three times with $^{14}CO_2$ and harvested while still green (Snyder 1985). The C/N and C/P ratios of the green litter were low compared to the element ratios of senescent wheat litter (Table 1.2). This could alter the effects of N and P addition on decomposition rate. This was the only labeled litter available, so in spite of the low C/N ratio, it was used to allow differentiation between carbon derived from litter and from SOM.

Table 1.2. Characteristics of wheat litter.

Mesh size	N (mg g^{-1})	C (mg g^{-1})	C/N	Label (dpm g^{-1})[1]
1 mm	20.1	384	19	4,800,000

[1] Disintegrations per minute.

Experimental Design

Treatments were arranged in randomized complete blocks with three replicates. Because it was impossible to incubate all the samples in the same incubator, randomized complete blocks were established to remove the effects of variable incubation conditions. Factorial experimental treatments consisted of texture (73%, 55% and 40% sand), soil water matric potential (-0.012, -0.033 and -0.30 MPa), nutrient availability (no nutrients added, 100 mg kg^{-1} N and 40 mg kg^{-1} P added), and time (10, 30, 60 and 90 d). The above treatments were run with surface litter only. A smaller experiment was established to assess the effect of litter placement on decomposition. For incorporated litter, factorial treatments were texture, nutrient availability, replicate and time (as described above). Soil water potential was -0.033 MPa for all experimental units in this experiment. Respiration was sampled 13 times during the incubation period on the subset of cores that were destructively sampled at 90 d. This made time a repeated measure for the soil respiration data.

Experimental soil cores were prepared by packing 67.8 g of soil into 4.8 cm diameter by 2.5 cm deep aluminum rings, equivalent to a bulk density of 1.45 g cm^{-3} (the average field bulk density across slope positions for these soils). Uniform bulk density was chosen to remove variability in total pore volume due to differences in bulk density. The goal was to control factors correlated to soil texture to isolate the specific effects of the different treatments. By standardizing bulk density and assuming uniform

particle density, all soils had similar total pore volume but different pore size distributions. Wheat litter was added at a rate of 2200 kg ha^{-1} (.40 g $core^{-1}$). Total C added was 2170 mg kg^{-1}.

For the incorporated litter treatment, litter was added to the soil before the cores were packed. All the cores (surface and incorporated litter) were then saturated with deionized water under a vacuum. After 2 hours of equilibration at -.01 MPa, suction was removed from the cores in order to add nutrient solution and apply surface litter. Ammonium sulfate (100 mg kg^{-1} N) and potassium phosphate (final P concentration of 40 mg kg^{-1}) were added by injecting four 1 mL aliquots halfway into the core. Different concentrations of potassium phosphate were used to obtain a final concentration of 40 mg kg^{-1} $NaHCO_3$ extractable P in each soil. Wheat litter was placed on the surface of the appropriate cores, saturated with deionized water and returned to pressure chambers to equilibrate for 3 d at 6°C to establish the soil water matric potential treatments. All setup and pressure plate equilibration was done at 6°C to prevent the onset of decomposition until samples were placed in individual incubation chambers. Saturating the litter before equilibrating the cores caused some leaching of litter C. This was the only way to establish litter moisture treatments that would parallel the matric potential treatments. After equilibration, the cores were placed in 1.9 L jars with 5 mL of 1*M* NaOH to trap CO_2 and incubated at 25°C in the dark for 90 d.

Sampling regime

Base traps were sampled for $^{14}C/^{12}C$-CO_2 weekly except during the first 10 d of the incubation, when they were sampled every 5 d. Total respiration was determined by titrating with 1.000*M* HCl (Coleman et al. 1978). For ^{14}C-CO_2, 1 mL of 1*M* NaOH was pipetted into a scintillation vial with 1.5 mL of water and 17.5 mL of Scintiverse BD (Fisher Scientific) scintillation cocktail. The sample was mixed and left in the dark for 1-2 hours. Counting was done for 10 minutes on a Beckman Tri-Carb 1500 liquid scintillation counter and corrected using a series of quenched standards. Soils were destructively sampled for inorganic nitrogen, phosphorus fractions and microbial biomass at 10, 30, 60 and 90 d.

Uniformity of ^{14}C label

Pulse labelling of plant material with ^{14}C-CO_2 can lead to uneven distribution of ^{14}C in plant carbon fractions. Distribution of the ^{14}C label in the litter was assessed by placing 0.4 g of wet litter (≈ -0.033 MPa) in a plastic beaker. The litter was incubated for 75 d at 25°C. Total respiration and ^{14}C-CO_2 were measured weekly using the techniques described previously. The specific activity of the respired CO_2 changed significantly during the 75 d incubation (Figure 1.1). The relationship between cumulative total C respired and cumulative ^{14}C-respired was used to predict the contribution of litter C to total respiration. The contribution of SOM to total respiration was calculated by difference.

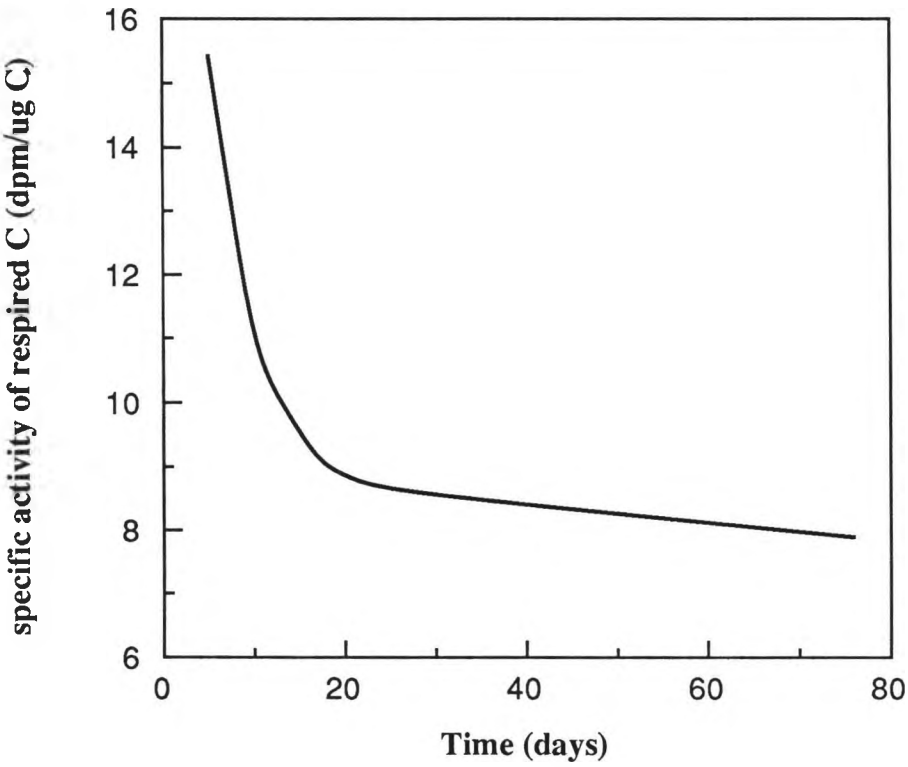

Figure 1.1. Change in specific activity of respired C when litter decomposes in the absence of soil for 72 d.

Statistical Analysis

Repeated measures ANOVA (SPSS, Inc.) was used to assess the main treatment effects, between treatment interactions and the interaction of the main treatments with time. All data analyzed with repeated measures were log transformed to homogenize the variance through time. If there was a significant treatment by time interaction, the 90 d incubation was broken down into 3 time periods (0-10, 11-51 and 52-90 d). Treatment effects on total C and ^{14}C respiration were determined for each time period using the MANOVA procedure with simple mean contrasts (SPSS, Inc.). Mean comparisons were done within each interval using the Bonferroni method to adjust the levels of significance based on the number of comparisons.

RESULTS

Results of this experiment are presented in two ways. Respiration of $^{14}CO_2$ is the indicator of litter decomposition in this experiment. Simultaneous measurements of $^{12}CO_2$ respiration are not useful as a measure of decomposition rate because of the contribution of SOM to this pool. It is necessary to measure $^{12}CO_2$ respiration for assessment of SOM mineralization and total microbial activity in the different soils.

^{14}C-Respiration

Soil texture had no effect on the rate of decomposition of surface applied litter. Total $^{14}CO_2$ loss from incorporated litter was greatest in the fine textured soil followed by the medium and coarse soil (Figure 1.2a). There was no significant texture effect on surface litter decomposition. Significantly more ^{14}C was lost from the -0.012 MPa matric potential, followed by the -0.033 MPa and -0.30 MPa matric potential (Figure 1.2b). The effect of matric potential occurred regardless of litter placement (only results for surface litter are shown). Nutrient addition had no effect on the rate of ^{14}C respiration from surface applied litter. Nutrient addition depressed the rate of ^{14}C loss when the litter was incorporated into the soil (Figure 1.2c). Litter placement had no effect on the overall rate of loss of ^{14}C (Figure 1.2d).

Temporal Variation in $^{14}CO_2$-Respiration

The coarse textured soil lost more ^{14}C from surface applied litter than the fine soil during 0-10 d (Table 1.3). After this time, there was little difference in the rate of ^{14}C loss from the three soils. By the end of the 90 d incubation, cumulative ^{14}C loss was the same regardless of soil texture. When litter was incorporated, the fine texture soil lost more ^{14}C than other textures during 0-10 d (Table 1.3). After this time period, no further textural effects occurred. The 0-10 d effect was large enough that cumulative 90 d ^{14}C respiration was significantly higher for the fine

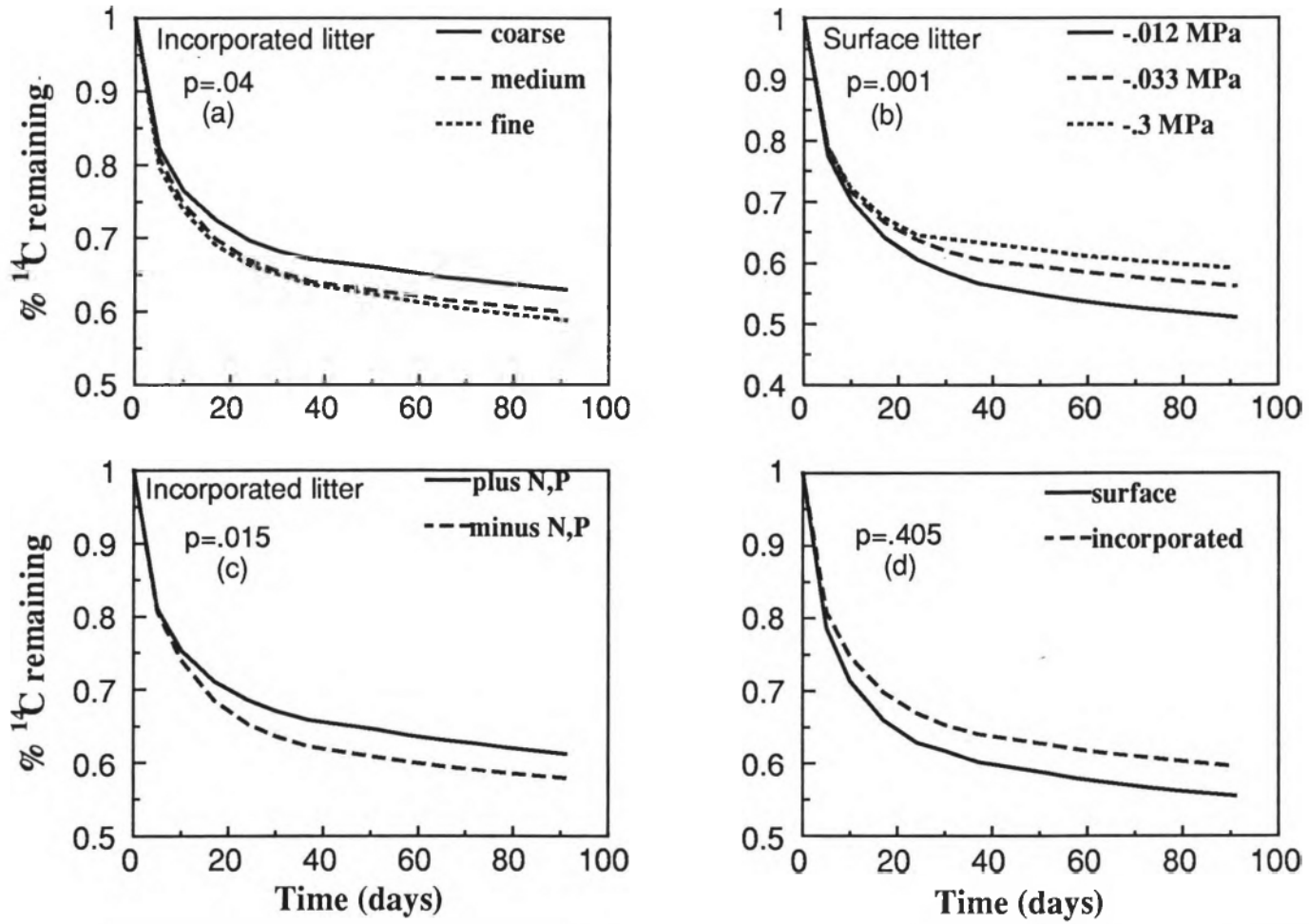

Figure 1.2. Significance of treatment effects from repeated measures ANOVA (a) Effect of soil texture on incorporated litter (b) Effect of soil matric potential on surface litter(c) Effect of nutrient addition on incorporated litter(d) Effect of litter placement.

Table 1.3. Proportion of ^{14}C lost from non-uniformly labeled wheat litter (see Figure 1) during 0-10, 11-51, 52-90, and 0-90 d. Mean comparisons were done within time periods and treatments using the Bonferroni correction of the p value. Total C added was 2270 μg C $(g\ soil)^{-1}$. Different letters represent significant treatment effects ($p \leq .017$). Surface vs. incorporated results are shown in a separate section at the bottom.

PROPORTION OF ^{14}C RESPIRED

TREATMENTS	Surface litter				Incorporated litter			
	0-10 d	11-51 d	52-90 d	0-90 d	0-10 d	11-51 d	52-90 d	0-90 d
TEXTURE								
73% sand	.298a	.126a	.028c	.457a	.234b	.102a	.030a	.370b
55% sand	.283b	.127a	.033b	.449a	.253ab	.114a	.030a	.400ab
40% sand	.279b	.134a	.036a	.429a	.262a	.111a	.034a	.412a
MATRIC POT.								
-.012 MPa	.298a	.148a	.037a	.489a	----	----	----	----
-.033 MPa	.278b	.119b	.030b	.408b	----	----	----	----
-.30 MPa	.284ab	.119b	.030b	.437b	----	----	----	----
NUTRIENT								
plus N,P	.283a	.119b	.032a	.438b	.246a	.104b	.033a	.387b
minus N,P	.290a	.141a	.033a	.452a	.259a	.128a	.029a	.421a
	Surface and incorporated litter							
LITTER PLCMT.								
surface	.287a	.129a	.032a	.448a				
incorporated	.253b	.116a	.031a	.400b				

textured soil relative to the coarse soil. The -0.012 MPa treatment lost more ^{14}C than either of the other two matric potential treatments during each time interval (Table 1.3). Nutrient addition depressed the rate of ^{14}C respiration during 11-51 d regardless of litter placement (Table 1.3). This effect was large enough that maximum 90 d ^{14}C respiration occurred without nutrient addition. Surface litter lost significantly more ^{14}C between 0 and 10 d than the incorporated litter treatment, after which there were no further significant litter placement effects (Table 1.3). Surface applied litter lost significantly more $^{14}CO_2$ over the 90 d incubation than did the incorporated litter due primarily to the differences at 0-10 d. This contradicts the result from the repeated measures analysis of litter placement effects (Figure 1.2).

Total C Respiration

Regardless of litter placement, maximum total 90 d respiration occurred in the fine textured soil (Table 1.4). For incorporated litter, fine textured soil had the highest total C respiration rate during 0-10 d. Soil texture had no effect during this time period for surface litter. This was due primarily to differences in mineralization of soil organic matter (see following section). During the 11-51 and 52-90 d period, the fine textured soil had the highest respiration rates of any soil for surface applied litter.

The -0.012 MPa matric potential treatment had higher total respiration rates than either the -0.033 or -0.30 MPa treatments. This

Table 1.4. Total C respired during 0-10, 11-51, 52-90 and 0-90 d. Mean comparisons were done within time periods and treatments using Bonferroni correction of the p value. Different letters represent significant treatment effects ($p \leq .017$). Surface vs. incorporated litter comparison shown in a separate section at the bottom of the table.

TREATMENTS	TOTAL RESPIRATION (µg/g)											
	Surface litter				Incorporated litter				No residue			
	0-10 d	11-51 d	52-90 d	0-90 d	0-10 d	11-51 d	52-90 d	0-90 d	0-10 d	11-51 d	52-90 d	0-90 d
TEXTURE												
73% sand	847a	546b	117c	1510c	821b	459a	128b	1407b	54b	86b	36c	175b
55% sand	868a	593b	166b	1626b	881ab	546a	160ab	1587ab	92a	179a	83b	352a
40% sand	869a	687a	222a	1769a	959a	562a	214a	1736a	110a	214a	117a	441a
MATRIC POT.												
-.012 MPa	897a	698a	184a	1780a	----	----	----	----	102a	194a	117a	415a
-.033 MPa	843b	570b	170a	1570b	----	----	----	----	87ab	179ab	78b	344a
-.30 MPa	842b	549b	149b	1540b	----	----	----	----	69b	104b	45c	222b
NUTRIENT												
plus N,P	878a	560b	157b	1595b	876a	507a	170a	1553a	----	----	----	----
minus N,P	843b	660a	180a	1674a	898a	579a	170a	1647a	----	----	----	----
	Surface and incorporated litter											
LITTER PLCMT.												
surface	843a	570a	170a	1570a								
incorp.[z]	887a	522a	167a	1577a								

result was identical to the result obtained for ^{14}C respiration. Nutrient addition depressed respiration at all time periods for surface litter except during 0-10 d (Table 1.4). There was no effect of nutrient addition on total respiration from incorporated litter. Total respiration loss from surface litter samples was lower during 0-10 d. In contrast, there was no effect of litter placement on cumulative 90 d total respiration (Table 1.4).

Soil priming

A single specific activity value could not be used to calculate the litter contribution to total respiration because of the non-uniformity of the ^{14}C label. To estimate the variability in specific activity of the litter, cumulative ^{14}C respiration from litter alone was compared to cumulative total respiration from litter in the absence of soil. Using non-linear regression (SPSS, Inc.), a quadratic function gave the best fit assuming a Y intercept of zero (Figure 1.3). Using this function, the litter contribution to total respiration could be predicted based on cumulative ^{14}C-respiration. Subtracting the litter contribution from total respiration gave the contribution of mineralized SOM to total respiration.

The addition of carbon substrate stimulated the mineralization of SOM (Figure 1.4). This increase in SOM mineralization is frequently referred to as the "priming" effect. The contribution of soil organic C to total respiration approximated 25% of total respired carbon for all soils. This was much greater than the amount of respiration when no litter was

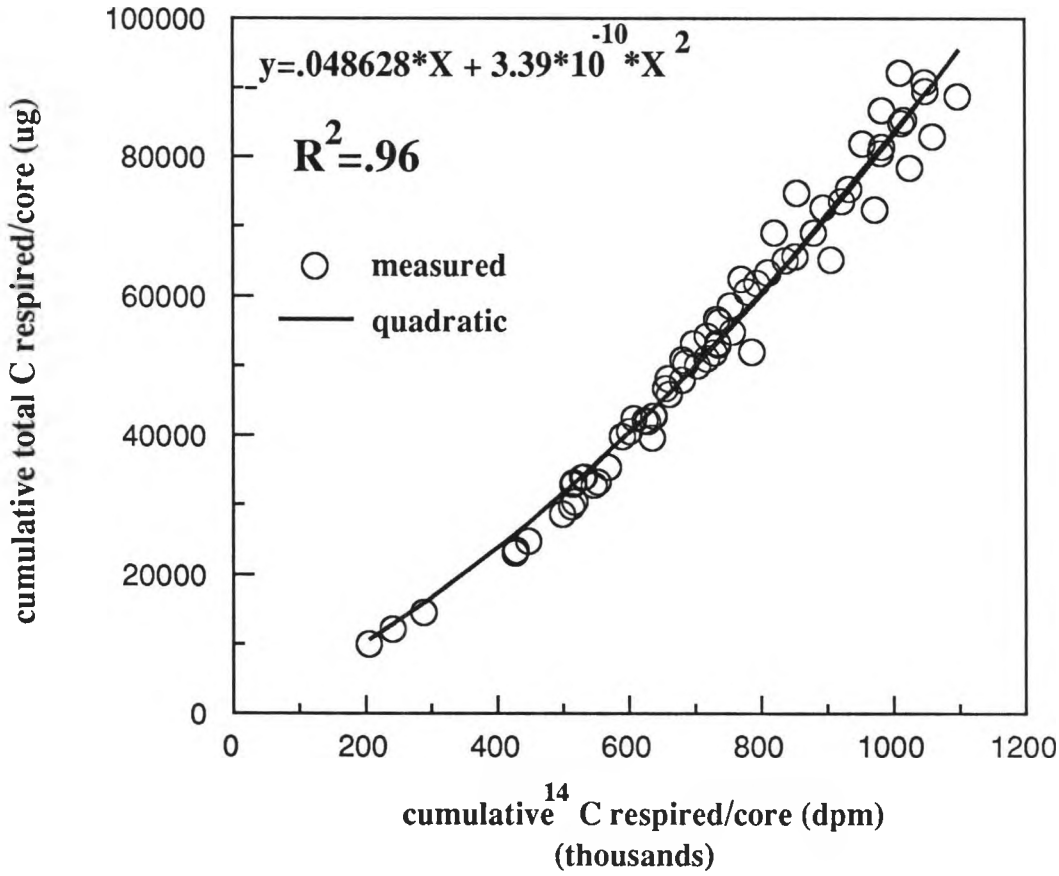

Figure 1.3 Cumulative ^{14}C- and total respiration from litter decomposing in the absence of soil. A straight line would indicate no change in specific activity of respired C.

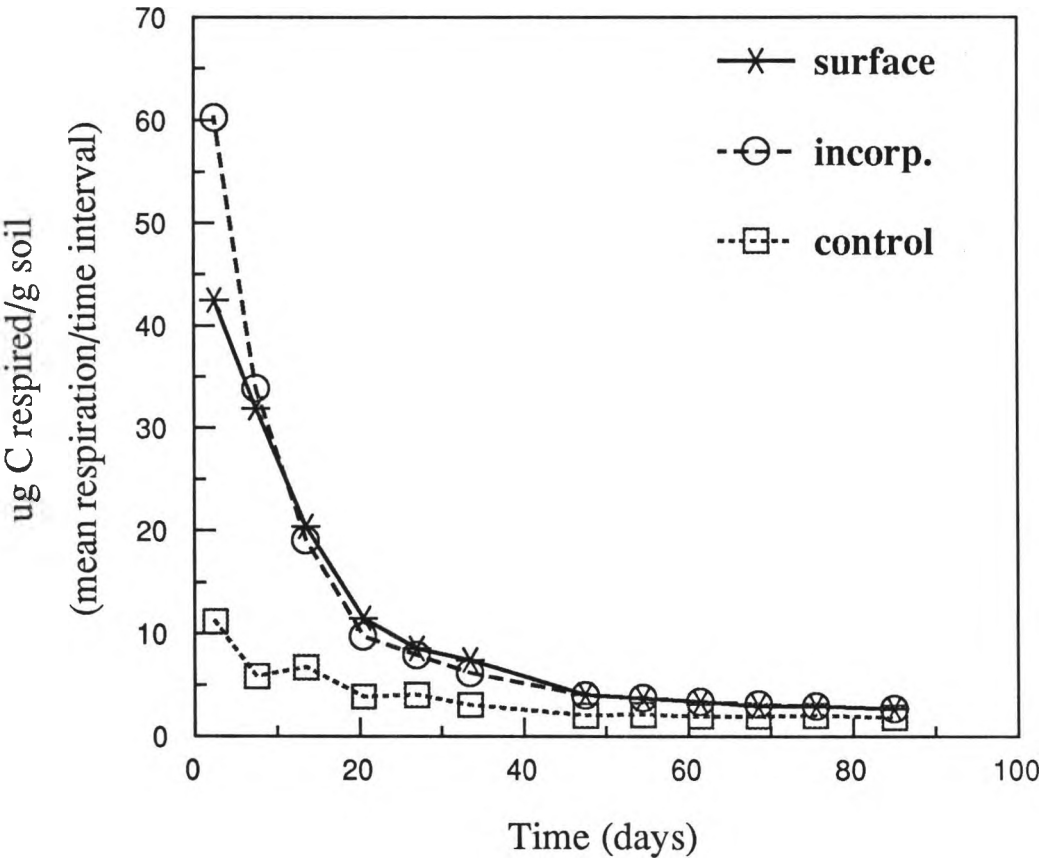

Figure 1.4. Contribution of soil organic carbon to total respiration for three litter treatments through time.

added (Table 1.4). Fine textured soil lost 8.9% of the total SOM pool compared to 11.1% and 15.9% for the medium and coarse soil, respectively. Even though it represented a smaller proportion of the total SOM pool, the greatest mineralization of SOM occurred in the fine textured soil because of the greater SOM pool size. When litter was incorporated, mineralization of soil organic carbon was significantly greater than when litter was applied to the surface, but only during the first 10 d of the incubation (Figure 1.4).

Water-filled pore space

When the respiration data were divided into 4 time periods, several significant texture by moisture interactions appeared (Figure 1.5). For a given soil texture treatment, ^{14}C respiration rate did not respond in a linear manner to changes in soil water matric potential. For the -0.033 and -0.30 MPa treatment, little difference existed between textures in the rate of ^{14}C respiration. Soil texture caused a large difference in ^{14}C respiration at -0.012 MPa. If one variable expressed the effect of this interaction on ^{14}C respiration, it would be possible to predict respiration rates across a range of soil texture and water potential. Percent water-filled pore space (%WFPS) is a function of soil texture and soil water potential, so it might be a good correlate with respiration rates in soils under different abiotic conditions. Bulk density and water content were controlled in this experiment, and from these data the %WFPS value for each combination of soil texture and soil water potential could be calculated.

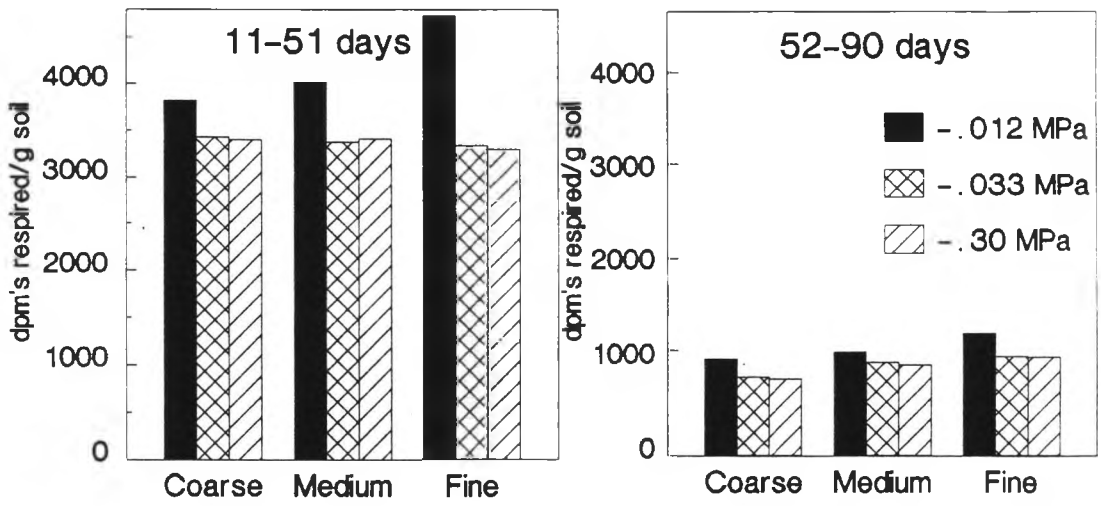

Figure 1.5. Significant texture by moisture interactions for ^{14}C respiration from surface applied litter during 11-51 and 52-90 days (dpm = disintegrations per minute of ^{14}C in respired C).

A strong linear relationship existed (independent of litter placement) between %WFPS and 90 d total respiration (Figure 1.6). For the incorporated litter treatments, there were three %WFPS levels (no matric potential treatments). The correlation between %WFPS and total respiration of carbon originating in the litter was not as strong for surface litter (r^2=0.33) as for incorporated litter (r^2=0.72) (Figure 1.7). Total respiration (litter plus SOM) correlated strongly with %WFPS regardless of litter placement (r^2=0.99 and 0.88 for incorporated and surface litter, respectively). Native SOM respired during the 90 d incubation increased with %WFPS regardless of litter addition or placement (Figure 1.8). The greatest effect occurred when no litter was added, followed by the effect on incorporated and surface litter treatments (slope = 7.54, 5.74 and 4.24 for control, incorporated and surface litter, respectively). The significance value for the regression between %WFPS and respired native SOM was significant only at p=0.08.

DISCUSSION

Temporal scale of decomposition experiments

The temporal scale of decomposition experiments is critical to the interpretation of significant results. A controlling factor may be important during the first 10 d of an experiment but have no effect on the final amount of plant litter remaining as SOM after 2-3 years. Even with the short time scale of this experiment, the importance of controls changed

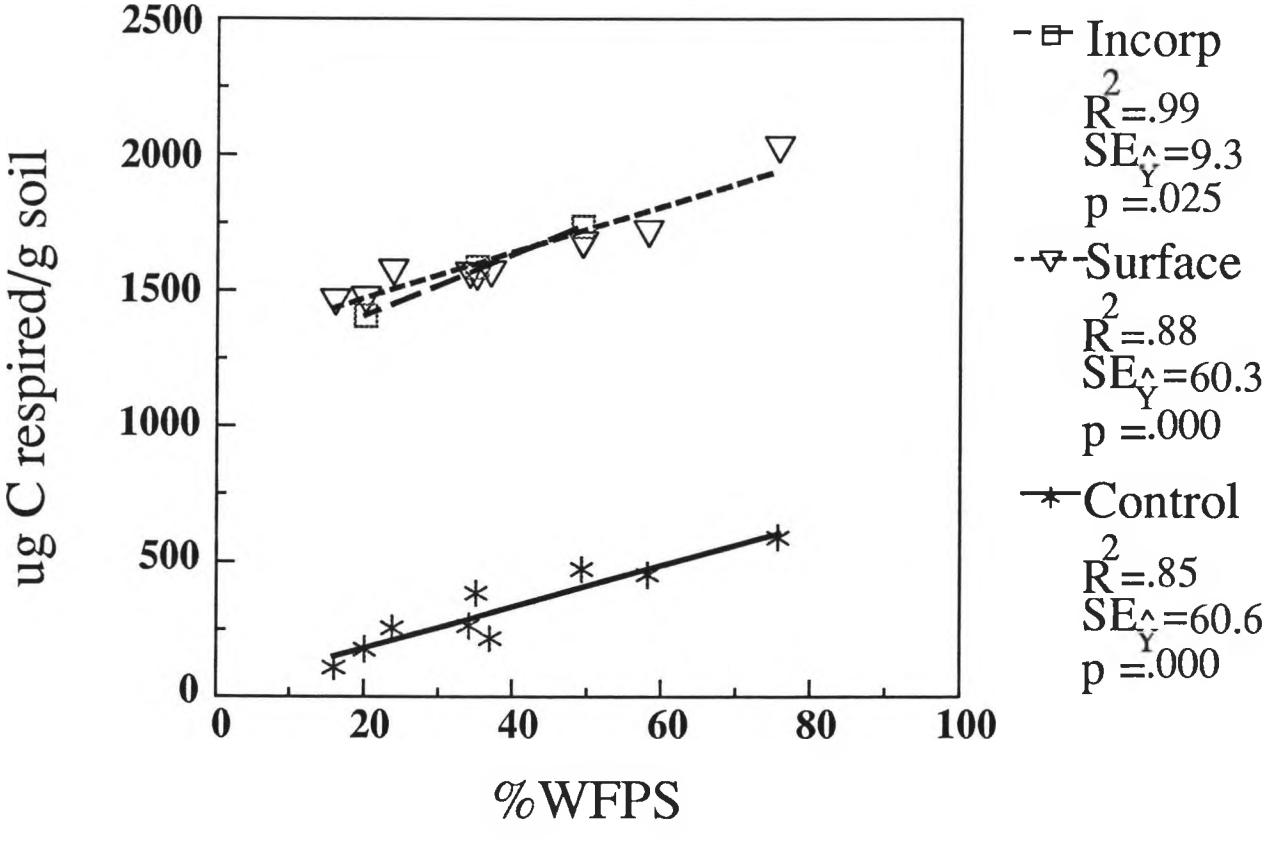

Figure 1.6. Effect of %WFPS on total cumulative 90 d respired C for the three litter treatments (each point is a mean with n=6).

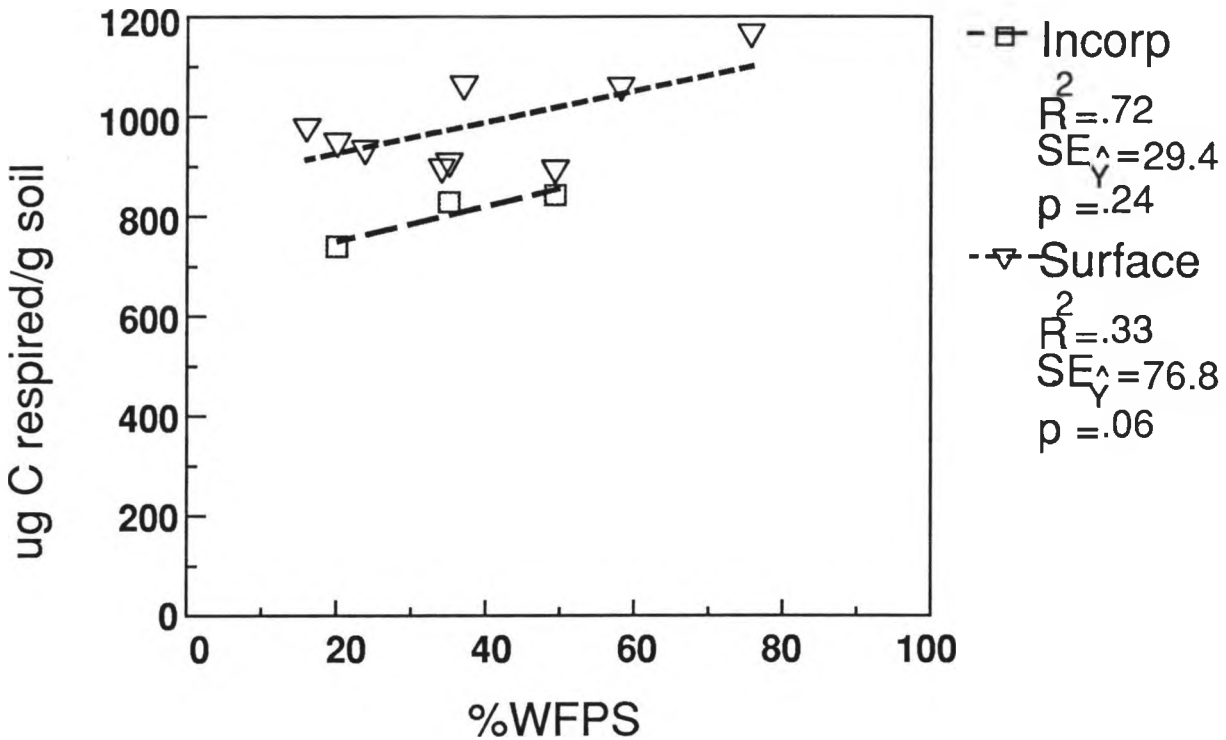

Figure 1.7. Effect of %WFPS on respired litter C (cumulative 90 d total). (each point is a mean with n=6)

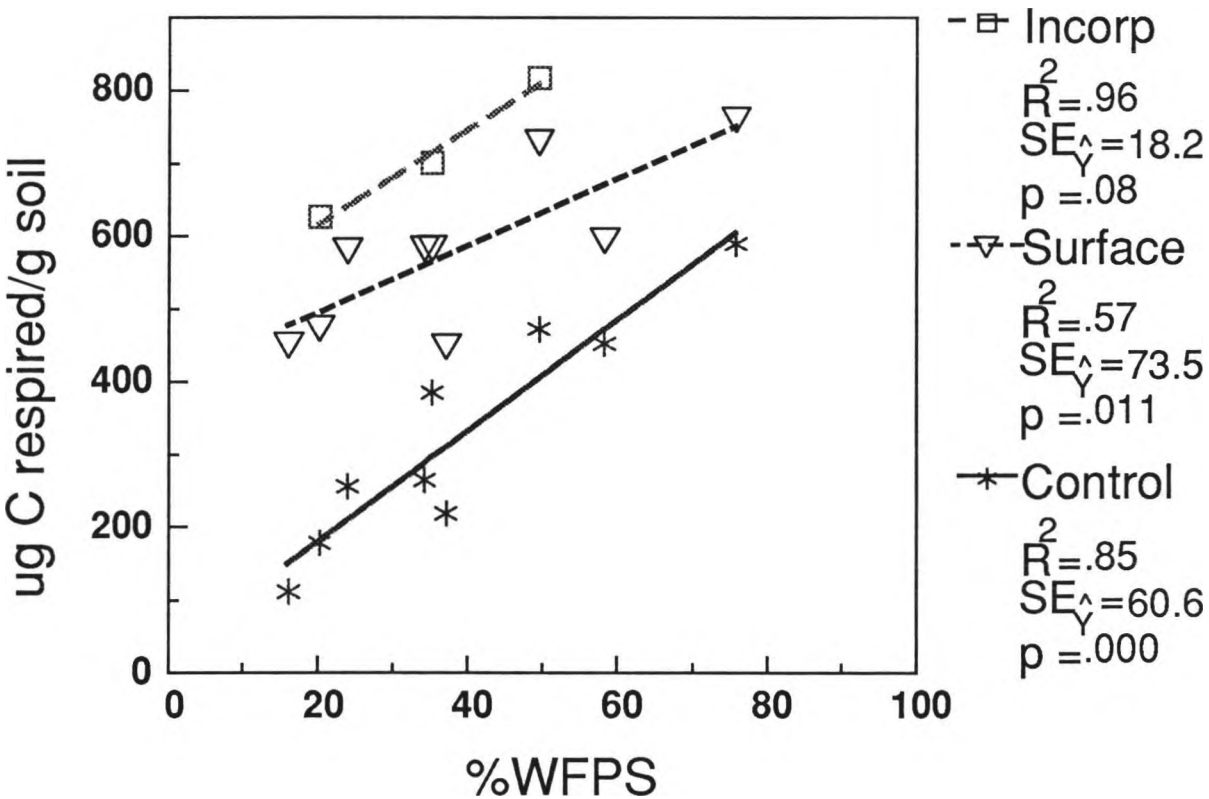

Figure 1.8. Effect of %WPFS on respired native soil organic C (90 d cumulative total) for the three litter treatments (each point is a mean with n= 6).

through time. During 0-10 d, the coarse textured soil lost more ^{14}C than either the medium or fine textured soil. The opposite effect occurred during the remainder of the incubation, leading to no net effect of soil texture (Table 1.3). For questions regarding microbial dynamics (i.e. mineralization and immobilization), short-term controls are important. If the primary interest is to describe the amount of plant litter remaining in SOM over longer time periods, short-term controls may be irrelevant. This experiment emphasizes the short-term controls on decomposition. The importance of these controls to long-term stabilization of soil organic C needs to be examined using long-term decomposition experiments.

Litter placement

The results of this experiment showed greater ^{14}C loss from the surface litter treatment during the first 10 d (Table 1.4). In field experiments, incorporation of litter into the soil often increases the rate of decomposition (Holland and Coleman, 1987; Cogle et al. 1987). In this experiment, the soil and litter (surface and incorporated) remained moist during incubation because of the high humidity maintained in the incubation chamber. Although the matric potential of the litter varied according to the matric potential of the soil, the relative humidity in the litter at each matric potential was very close to 100%. By maintaining the relative humidity in the surface litter close to 100% during incubation, microorganisms utilizing this material would avoid desiccation.

During the early stages of decomposition, soil slowed rates of decomposition (as measured by ^{14}C respiration) possibly through the stabilization of microorganisms or microbial metabolites. Tester (1988) found that during laboratory incubations, microorganisms indigenous to plant litter were responsible for most of the early (0-10 d) decomposition of incorporated wheat litter, after which soil microbes became the dominant group of organisms. In the field, surface litter is repeatedly wetted and dried, usually lowering the rate of decomposition relative to incorporated litter. The lack of contact between litter and soil particles apparently does not retard decomposition of surface litter as long as litter moisture levels are maintained. It is critical to keep in mind how the method used to measure decomposition might influence this result. Incorporated litter might have faster mass loss, but because of the intimate contact of the litter with the soil there is greater potential stabilization of litter C during decomposition. When using the respiration of $^{14}CO_2$ as an indicator of decomposition, stabilization could lead one to infer slower decomposition for incorporated litter.

Water-filled pore space as a control on decomposition

The %WFPS of a soil appears to regulate the mineralization of SOM to a greater extent than it does the decomposition of plant litter. This implies that the distribution of water in the soil matrix, not the soil water content, is the important control of %WFPS. As %WFPS increases, more of

the pore volume is habitable by microorganisms. Higher habitable pore volume should increase the rates of SOM mineralization and decomposition, especially for incorporated substrates. A different mechanism must be responsible for the effect of %WFPS on decomposition of surface litter, or else the effect is delayed until the litter C enters the soil matrix. It is possible that %WFPS controls the activity of fungi whose hyphae extend from the soil into the litter. A stronger relationship existed between %WFPS and substrate C respired from surface litter during 52-90 d (r^2=0.92) than during 0-10 d (r^2=0.003). This supports the notion that %WFPS regulates decomposition of surface litter only after some of the litter C has entered the soil matrix and soil microbes become the dominant decomposers.

The %WFPS and soil water potential are very different measures of soil water availability. Only %WFPS says something about the spatial distribution of soil water in the soil matrix. Most soil microorganisms require water to sustain activity. As %WFPS increases for a given soil, more pores (and smaller pores) become filled with water. This in effect increases the amount of habitable pore volume exploitable by soil microorganisms. The rate of microbial activity is determined by a delicate balance between O_2 diffusion to the individual cells, substrate movement (diffusion or mass flow) to cells, and removal of potentially toxic metabolic products. As water content (%WFPS) increases, the soil environment becomes more conducive to maintaining microbial populations. At some

point, O_2 diffusion into the soil becomes inhibited, which should reduce the rate of microbial activity as measured by CO_2 production. The litter used in this experiment was ground to pass through 1 mm mesh. A 1 mm soil pore is a very big pore that will drain fairly quickly when a matric potential is imposed on a previously saturated soil. That may be the reason for the apparent control of %WFPS on SOM mineralization as opposed to litter decay. Only in the fine textured soil (with the highest values of %WFPS) did it become apparent that %WFPS was strongly influencing litter decay (Figure 1.5).

There was no decrease in total respired C (90 d) as %WFPS varied from 16% to 75%, the maximum value in this study (Figures 1.6 and 1.7). Linn and Doran (1984) and Doran et al. (1988) have shown that relative CO_2 production increases as WFPS increases up to approximately 60%, beyond which relative respiration decreases and N_2O production increases. They fit a quadratic function to data obtained from soils of different textures. For soils with sand content >50%, they found a slightly different function gave a better regression fit (peak relative respiration at 54% WFPS). All soils at a given %WFPS had comparable relative respiration rates, coarse soils being slightly different than fine ones. In this study, each soil was not represented at each level of %WFPS. By comparing the relationship between %WFPS and respiration rate for each soil (compare the slopes of the regression line), the relationship proved to be the same regardless of the texture of the soil. Therefore it was reasonable to plot the

data from all three soils on the same graph even though the range in sand content suggested a need for two different functions. The relationship proposed by Doran et al. (1988) applied to mineralization of native organic matter, not to the loss of added substrate C. Loss of CO_2 from the controls used in this experiment did not decrease above 55-60% WFPS. Some drying of the soil cores occurred during the incubation. The change was not, however, enough to lower the maximum %WFPS below 60%. More recent work (Skopp et al. 1990) shows that peak respiration rates occur somewhere closer to 70% WFPS, which is fairly close to the maximum value used in this study.

The linear function relating %WFPS to 90 d cumulative respiration had a Y intercept close to zero only when no litter was added. Assuming that at 0% WFPS there would likely be no microbial activity, the function relating %WFPS to respiration (decomposition) must be non-linear (or have a different slope) somewhere between 0% and 16% WFPS (Figures 1.6-1.8). The only regression that had an intercept close to zero was for respired native SOM without substrate addition. In this experiment, %WFPS and microbial activity were positively correlated. It is not clear what the relationship would be at %WFPS values less than 16% when substrate is added. It would appear that the relationship must become nonlinear below this point in order to intersect the origin. This nonlinearity has been shown to exist for some soils even when no substrate is added (Skopp et al. 1990).

Soil texture

The results of this experiment showed greater respiratory loss of ^{14}C and total C in the fine soil throughout most of the incubation (Tables 1.3 and 1.5). Higher clay content increases stabilization of residue C into SOM, resulting in a smaller percent loss (Sorenson 1981; Merckx et al. 1985; Parton et al. 1987). This may be due, in part, to the greater surface area and pore volume present as clay content increases. By maintaining constant bulk density, total pore volume was constant for each of the soils. This could be construed as an unrealistic way to compare soils of different texture. However, if the main effect of higher clay content on decomposition results from differences in pore volume, one way to test this hypothesis is to remove the difference. As discussed above, the availability to soil organisms of habitable pore volume probably regulates mineralization of SOM and incorporated litter decomposition. This might explain why decomposition was not faster in the coarse soil, but it does not explain more rapid decomposition in the fine soil.

The soil pore volume habitable by microorganisms changes with concomitant changes in pore size distribution and matric potential (Elliott et al. 1980). By compressing the fine textured soil to a higher bulk density than that found in the field (1.45 vs. 1.32), the soil environment may have become more favorable for microbial activity, especially bacteria. Soil bacteria exist in water films that coat the surfaces of soil aggregates. They depend on these films to prevent desiccation and permit movement to new

substrates. At a given matric potential, the soil with more small pores will have a higher volumetric water content and higher %WFPS. This could create an environment more suitable for bacterial growth. Bacteria have a lower assimilation efficiency than fungi (Alexander 1977), which could explain the greater respiratory loss of ^{14}C from the fine textured soil.

Higher %WFPS may also cause decreased microbial efficiency by increasing the number of anaerobic microsites. If the efficiency of the decomposer community decreases due to low O_2 tension, loss of substrate C would increase (assuming the decomposition rate stayed constant). One pathway for this greater loss of C is via CO_2 production. Over the range of matric potential treatments used, the fine textured soil had the highest mean %WFPS (53% vs. 39% and 25% for the medium and coarse texture soil, respectively). This would explain the lower percent remaining substrate C and more rapid ^{14}C loss in the fine textured soil. Mass loss may have been unaffected by variability in soil texture or matric potential. Using an indirect method for measuring decomposition makes it difficult to say what is happening to litter mass loss.

The initial rapid growth of the microbial biomass after substrate addition may regulate both short- and long-term decomposition. Factors that regulate the initial rapid growth phase would ultimately regulate decomposition rate. Labile C can limit microbial growth during early stages of decomposition when other factors are not limiting (Reinertsen et al. 1984; Knapp et al. 1983). This can limit short-term rates of decomposition and

may be important to long-term rates of decomposition. Soil texture may also regulate short-term decomposition by limiting the maximum biomass that a soil can sustain. As discussed above, habitable pore space varies as a function of texture and moisture. As clay content increases at a fixed soil water potential, habitable pore space increases. Finer textured soils may therefore support a larger microbial biomass, leading to faster rates of decomposition. Soils with higher clay content contain higher levels of SOM, which could enhance the growth of microbes utilizing SOM as a substrate during litter decomposition (see next section).

Mineralization of soil organic matter

Addition of a relatively high quality substrate (C/N=19) stimulated the mineralization of native organic matter. The proportion of total respiration attributed to SOM was between 10% and 15%. No satisfactory mechanism has explained the priming effect on native soil organic C. Parnas (1976) proposed a mechanism based on substrate C/N ratio control of microbial growth. She concluded that maximum microbial growth would occur with a substrate C/N ratio of approximately 25, leading to the greatest mineralization of native soil organic C. This assumes that protection of certain plant compounds does not vary between species of plants. Wheat litter used in this study had a C/N of 19, close to the proposed optimal growth C/N proposed by Parnas (1976). If priming is a growth related phenomenon, it implies that a limiting resource would slow microbial

growth and subsequent priming. Very few studies have investigated the combined effect of C and N availability on SOM mineralization. The studies that have been done look at the independent effects of inorganic N addition or labile C_{org} addition (Jenkinson et al. 1985; Broadbent and Norman, 1946). It is important to understand the conditions that lead to significant soil priming, especially for the conceptualization and construction of decomposition and SOM simulation models.

CONCLUSIONS

Soil texture is a factor that influences many biotic and abiotic characteristics of the soil environment. Water availability, organic matter content, aggregation, surface area, porosity and cation exchange capacity are examples of factors controlled by or linked to soil texture. All of these factors impact rates of decomposition and organic matter dynamics. The results of this work suggest that the role soil texture plays in short-term decomposition and SOM formation relates to its effect on the spatial characteristics of the soil ecosystem. By manipulating the bulk density of the soil, the effect of soil texture could be reversed from that noted in Sorenson (1981). The relationship between %WFPS and respiration further demonstrates the important role habitable pore space plays as a control on soil processes.

Results from this experiment lead to the conclusion that the effect of soil texture on decomposition differs across time scales. The usual

assumption is that heavier textured soils stabilize more organic C. When litter was incorporated, more litter C was lost from the fine textured soil, the main effect occurring during 0-10 d. When litter was placed on the surface, more litter C was lost from the sandier soil during 0-10 d, but by the end of 90 d there was no effect of texture. When there is an adequate supply of nutrients and moisture, surface litter can decompose as quickly or faster than incorporated litter. When soil water potential increases, decomposition rates increase regardless of soil texture. This effect of water potential appears to be very nonlinear, especially across a gradient of soil texture. In most cases, there was little difference in decomposition rate between -0.30 and -0.033 MPa, but a large increase at -0.012 MPa. This interaction of soil texture with water potential can be expressed as one variable, %WFPS, that seems to predict adequately rates of decomposition and SOM mineralization. Finally, adding a fairly high quality plant litter to the soil appears to stimulate the mineralization of SOM. The magnitude of this effect varies with texture and %WFPS. The fine texture soil lost more SOM than did the other two soils. There was greater SOM mineralization with increasing %WFPS. For short-term dynamics during litter decay, it would appear that texture can have the opposite effect predicted from long-term decay rates. The interaction of texture with water potential to create habitable pore space may be the most important effect of texture during short-term litter decomposition experiments.

The question arises whether three month incubations provide useful insights into the decomposition process. In the field, plant litter may take two or more years to thoroughly decompose. Do results from this type of incubation provide any useful insights? I think they do, especially for assessing how different factors control decomposition through time. Although the effect of texture may be measured after litter has completely decomposed, the effect may have occurred early in the decomposition process. Short term incubations that speed the decomposition of plant material provide the opportunity to address temporal changes in controlling factors during the 50-60% weight-loss period for plant litter. I think there is also a need for long-term incubations to address long-term controls.

Several questions arise as a result of this experiment. What would be the effect on decomposition and SOM dynamics of changing bulk density? Does clay mineralogy play a significant role in dynamics of SOM, and if so, is it necessary to characterize clay mineralogy before the role of soil texture can be predicted for a specific soil? Is the size of the initial labile SOM pool a factor that can influence litter decay rate? Finally, does litter quality affect the degree to which SOM is mineralized during decomposition? What factors contribute to the presence or absence of soil priming following substrate addition? It is important to understand these controls on organic matter dynamics before the effects of soil texture can be adequately represented in simulation models of organic matter dynamics.

CHAPTER II.

SIMULATING THE EFFECTS OF SOIL TEXTURE AND ELEMENT INTERACTIONS ON DECOMPOSITION AND SOM DYNAMICS

INTRODUCTION

The CENTURY model (Parton et al. 1987) incorporates the effect of soil texture on soil organic matter (SOM) dynamics and litter decomposition by using different stabilization efficiencies based on percent clay content. The higher the clay content, the greater the stabilization of SOM during decomposition. This concept is free of the complexity underlying textural control of decomposition. As discussed in Chapter 1, litter decomposition was faster in the soil with higher clay content. This is opposite to the predicted result based on the relationship between clay content and SOM stabilization in CENTURY (Parton et al. 1987). There was also a significant contribution of native SOM to total respiration during substrate decomposition that varied across soil texture treatments. Increased moisture availability (matric potential) stimulated rates of decomposition. The effect of soil moisture was greatest in the fine textured soil (greater treatment differences). Under the conditions of the experiment described in Chapter I, higher clay content did not increase litter C stabilization. There were, however, significant effects of soil texture on litter decomposition,

especially when the litter was incorporated into the soil. The mechanism of this effect is complex given the number of other soil physical factors that vary in conjunction with soil texture. Simulation models can be used to integrate multiple controls in a way that permits hypothesis testing and hypothesis generation without having to do laborious field or lab experiments. One of the important goals of this modeling exercise was to integrate the interactions of C, N and P as well as other important factors that control decomposition. This chapter focuses on the construction of a decomposition model that represents the individual effects and the interaction of several controls on decomposition.

OBJECTIVES

The primary goal of this simulation exercise was to explicitly represent specific controls on decomposition. Is it feasible to represent factors like moisture availability without considering the interaction with soil texture? How can the effect of soil texture be represented during short-term incubations? How important are initial conditions such as bulk density, labile soil organic carbon (SOC), and litter C/N ratio on decomposition rates? This model provides a means for collecting and integrating several potentially important controls on decomposition. More specifically, the model represents the interactions of C, N, and P during decomposition. The model provides a means for testing ideas about element interactions and texture effects across gradients of soil texture, litter

quality, soil water potential and nutrient availability. Finally, the similarity of long- and short-term controls on decomposition can be tested with the model. Are the important controls on short-term decomposition rates similar to long-term controls? Many of these questions can only be addressed using a simulation model.

MODEL CONSTRUCTION

Description of structure and function

The system diagram for the model is shown in Figure 2.1. All computer code is contained in Appendix 1. The dynamics of decomposition center around the dynamics of the microbial biomass. Sources, sinks and state variables are labelled C1-C7 (same for N and P) for convenience of equation formulation. The model uses a daily time step. For most of the C flows, N is assumed to flow in proportion to the amount of C flux. Some of the P flows are not directly linked to carbon (Figure 2.1). See Tables 2.1 and 2.2 for definitions, units and values of the parameters and initial conditions for the C and N component of the model. The P submodel was developed by another person working on this project (Steve Huffman **personal communication**) and therefore will not be discussed in this chapter.

The first process in the model is to divide the residue into 2 pools, one composed of more resistant compounds (C1) (lignin etc.) and the other composed of more labile organic compounds (C2) (proteins, simple sugars

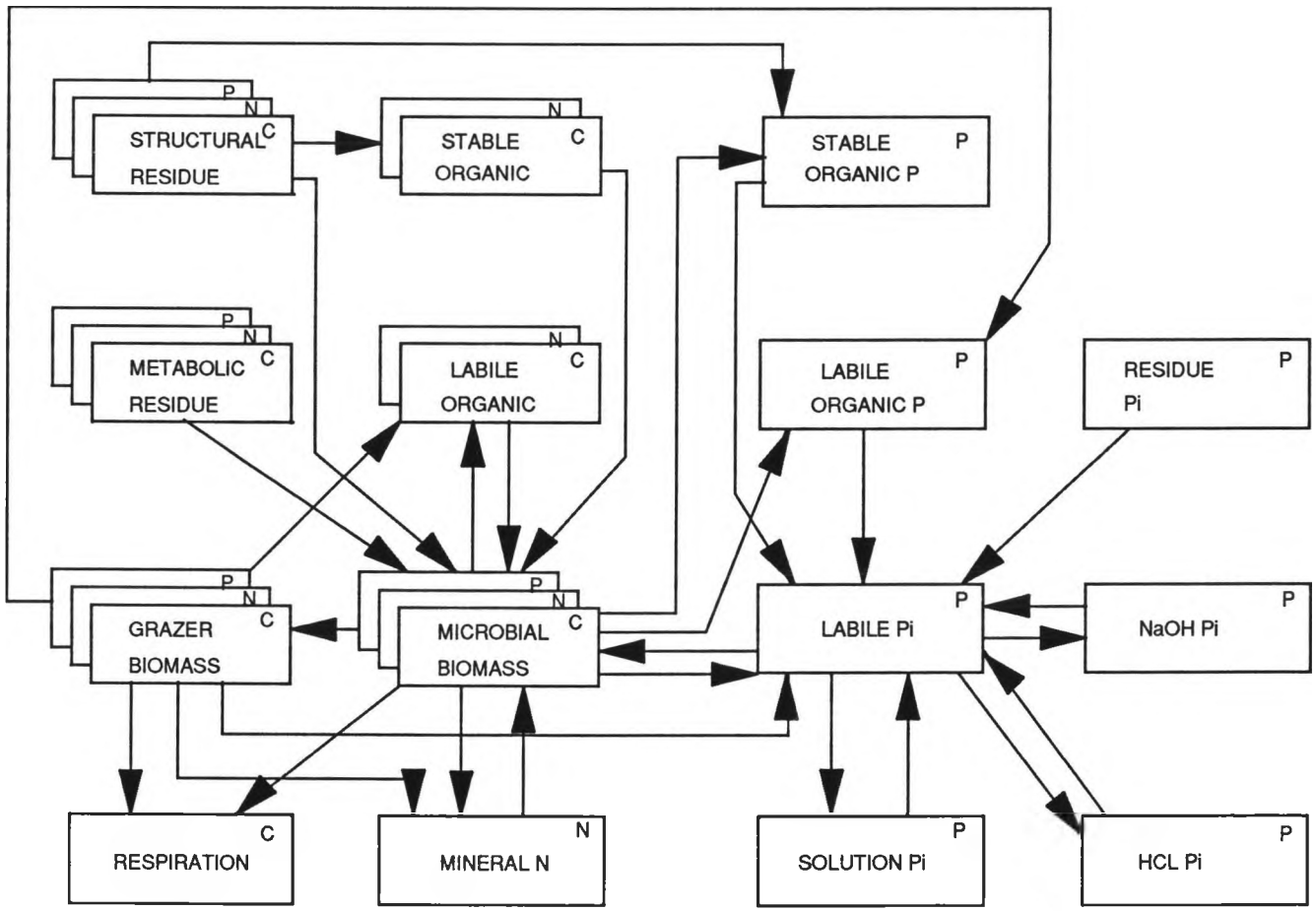

Figure 2.1. Conceptual diagram of C, N, and P flows and interactions during decomposition.

Table 2.1. Fixed parameter values for the simulation model .

Name	Value	Units	Description
VMC1	1	mg kg^{-1} $time^{-1}$	Vmax for Michaelis-Menten expression, structural C to microbial C.
KMC1	15000	mg kg^{-1}	Half saturation constant for M-M expression, structural C to microbial C.
VMC2	.7	mg kg^{-1} $time^{-1}$	Vmax for M-M expression, metabolic residue C to microbial C.
KMC2	300	mg kg^{-1}	Half saturation constant for M-M expression, metabolic C to microbial C.
VMC3	2	mg kg^{-1} $time^{-1}$	Vmax for M-M expression, grazer uptake of microbial C.
KMC3	300	mg kg^{-1}	Half saturation constant for M-M expression, grazer uptake of microbial C.
VMC4	.7	mg kg^{-1} $time^{-1}$	Vmax for M-M expression, labile SOM to microbial C.
KMC4	300	mg kg^{-1}	Half saturation constant for M-M expression, labile SOM to microbial C.
VMN6	.02	mg kg^{-1} $time^{-1}$	Vmax for M-M expression, microbial uptake of mineral N.
KMN6	5	mg kg^{-1}	Half saturation constant for M-M expression, microbial uptake of mineral N.
KC04	.04	$time^{-1}$	Grazer C to labile SOC. Mineralization associated with grazer activity.
KC06	.02	$time^{-1}$	Maintenance respiration from grazers.
KC36	.02	$time^{-1}$	Maintenance respiration from microbes.

Table 2.1. Continued.

Name	Value	Units	Description
KC34	.02	$time^{-1}$	Death of microbial biomass and contribution to labile SOM.
KC53	.00002	$time^{-1}$	Microbial uptake of resistant SOM.
YC13	.3		Yield coefficient, proportion of C that flows from plant structural C to microbial C incorporated into biomass.
YC23	.55		Yield coefficient, proportion of C that flows from plant metabolic C to microbial C incorporated into microbial biomass.
YC30	.2		Yield coefficient, proportion of C that flows between microbes and grazers that is incorporated into grazer biomass.
YC43	.4		Yield coefficient, proportion of C that flows from labile SOM to microbial C that is incorporated into microbial biomass.
YC53	.2		Yield coefficient, proportion of C that flows from resistant SOM to microbes that is incorporated into microbial biomass.
STABC	.2	$time^{-1}$	Stabilization coefficient, proportion of structural residue C stabilized into resistant SOM at.
CNMAX	20		Maximum C/N ratio of microbial biomass.
CNMIN	5		Minimum C/N ratio of microbial biomass.
STCN	100		C/N ratio of litter structural component.

Table 2.1. Continued.

Name	Value	Units	Description
MECN	8		C/N ratio of litter metabolic component.
PROTM	50	mg kg^{-1}	Protected level of microbial biomass.
PROTG	2	mg kg^{-1}	Protected level of grazer biomass.
CN0	5		C/N ratio of grazers.
PART	.7		Partitioning of grazer C to labile organic C (defecation).
STABZ	.01		Incorporation of grazer metabolites into resistant SOM.
DT	.1		Time step for solving differential equations.

Table 2.2: Initial conditions for nitrogen and carbon state variables and adjustable parameter values.

Name	Value	Units	Description
RESCN	19		Residue C/N ratio, initial value.
RESC	2171	mg kg^{-1}	Initial value for residue C.
WFPS	.75		Proportion of soil pore volume filled with water (this value for fine soil at -.012 MPa.
C0	15	mg kg^{-1}	Grazer biomass C.
C1	0	mg kg^{-1}	Structural plant C (calculated based on the C/N ratio of the litter.
C2	0	mg kg^{-1}	Metabolic plant C (calculated based on the C/N ratio of the litter.
C3	100	mg kg^{-1}	Microbial C (value for fine textured soil).
C4	500	mg kg^{-1}	Labile SOC (estimated value for fine textured soil).
C5	7400	mg kg^{-1}	Resistant SOC (estimated value for fine textured soil).
C6	0	mg kg^{-1}	Respiration.
N0	3	mg kg^{-1}	Grazer biomass N.
N1	0	mg kg^{-1}	Structural plant N.
N2	0	mg kg^{-1}	Metabolic plant N.
N3	10	mg kg^{-1}	Microbial N (value for fine textured soil).
N4	10	mg kg^{-1}	Labile SON (estimated value for fine textured soil).
N5	740	mg kg^{-1}	Resistant SON (estimated value for fine textured soil).

Table 2.2. Continued.

Name	Value	Units	Description
N6	5	mg kg^{-1}	Soil mineral N.
NA	30	mg kg^{-1}	Inorganic N in plant litter (value for C/N=19 litter).
SAC1	10.1		Specific activity of resistant plant C.
SAC2	18.		Specific activity of metabolic plant C.

etc.). This division is based on the C/N ratio of the plant residue (RESCN) and the C/N ratio of the metabolic pool (MECN=8) and the structural pool (STCN=100) (McGill et al. 1981). The equation used to partition C into the structural pool is

C1=RESC*(STCN-(MECN*STCN/RESCN))/(STCN-MECN)

The metabolic pool of carbon is calculated as the difference between the total carbon pool and the calculated structural C pool.

Decomposition kinetics are often described using first order, single exponential models. Because of the heterogeneous chemistry of plant residues (including roots), double exponential models do a better job of predicting decomposition kinetics over a longer time period (Hunt 1977; Voroney et al. 1989). A double exponential model represents the decomposition of two different C pools by using a different decay constant for each pool. After litter was partitioned to structural and metabolic C, two Michaelis-Menten (M-M) expressions were used to simulate microbial utilization of the two C sources. The M-M expressions for the flow rate from structural C to microbial C (C1TOC3) and metabolic C to microbial C (C2TOC3) are

C1TOC3=(C1*C3*VMC1)/(C1+KMC1)
C2TOC3=(C2*C3*VMC2)/(C2+KMC2)

A portion of the carbon flowing from C1 and C2 is incorporated into microbial biomass while the rest is respired away. The C utilization efficiency (YC##) of microorganisms is based on cellular physiology and

substrate quality. The differential equations used to represent the amount of C1 and C2 respired by microorganisms are

$$dC6/dt=YC13*C1TOC3$$
$$dC6/dt=YC23*C2TOC3$$

where YC13 and YC23 are yield coefficients that control how much C is respired. These yield coefficients are assumed to stay constant. Values for these parameters are shown in Table 2.1.

Microbial C flows to several soil C pools depending on the process. Some is consumed by grazers (C0). Grazer community structure has been simplified for purposes of this model. In soil, grazer populations consist of numerous organisms with great diversity of form, function and physiology. For a more complete description, see Hunt et al. (1987). The equation for consumption of microbes (C3TOC0) is again a source-sink driven M-M expression

$$C3TOC0=(C3*C0*VMC3)/(KMC3+C3)$$

A certain portion of the ingested microbial biomass was used for growth and maintenance of the grazer biomass, the remaining portion was respired. A fixed portion of the grazer carbon then enters both the labile organic (C4 and N4) pools through death and defecation. Maintenance respiration is represented separately from respiration associated with microbial consumption (C0TOC6). The following differential equation represents the dynamics of the grazer population

$$dC0/dt=YC30*C3TOC0-C0TOC6-C0TOC4$$

Microbial carbon flows directly into labile SOC (C4) at a constant rate via microbial death and metabolite production. A fixed proportion of these two flows is incorporated into the resistant SOC pool (C5). The two SOC pools in this model are a simplification of the three pool structure used in other SOC models (Parton et al. 1987). For the purposes of this model, material that flows into the resistant SOC pool has such a long turnover time that its impact on the model as a source of C, N or P is minuscule. The labile pool is continuously reutilized by the microbial biomass. Some is incorporated into biomass (C3), the rest is respired away (C6) as shown below

C4TOC3=(C3*C4*VMC4)/(KMC4+C4)
dC3/dt=YC43*C4TOC3
dC6/dt=(1-YC43)*C4TOC3

The other input of carbon into the resistant SOC pool is directly from the plant litter. This input consists of resistant plant compounds such as lignin. This is accomplished by moving a constant proportion of the flow from structural C to microbial C into the resistant SOC pool. A more realistic way to represent this flow would be to base it on the lignin and nitrogen content of the litter (Parton et al. 1987). I did not have data on lignin content, so an approximate value from the literature was chosen to represent the flow (C1TOC5). Respired C (C6) is derived from four different sources as shown in the next equation.

dC6/dt=((1-YC13)*C1TOC3)+((1-YC23)*C2TOC3)+((1-YC43)*C4TOC3)+
((1-YC37)*C3TOC0)

Physical controls on decomposition

One of the primary objectives of this model was to incorporate the control of soil physical properties on decomposition. Results presented in Chapter 1 demonstrate that percent water-filled pore space (%WFPS) can be used to predict rates of decomposition and SOM mineralization. Models of SOM dynamics often incorporate some type of soil moisture model because soil moisture has a major influence on microbial activity. By combining the effect of soil water potential and soil texture into one variable, it is much easier to represent these two important controls. The control of %WFPS is likely non-linear at the low and high end, respectively, of %WFPS values. Within the range of %WFPS values used in this model, the effect will be considered linear (see Figures 1.6, 1.7 and 1.8).

Incorporating the effects of %WFPS in the model was another challenge. van Veen et al. (1985) suggest 4 ways soil structure and texture might impact microbial populations. One possibility is a change in microbial growth efficiency. This effect was also suggested by Sorenson (1981). Another possibility is an alteration of substrate availability either by restricting organism mobility or the movement of substrates carried in the soil solution. Finer textured soils have greater surface area available for stabilizing organic C, lowering the rate of C loss via respiration. Depending on the method used to measure decomposition, this can be perceived as lowering rates of decomposition (Sorensen 1981). Finally, the thickness of the water film surrounding soil particles regulates the

movement of potentially toxic cell metabolites away from live cells. Percent water-filled pore space is not as good at predicting rates of loss of litter C from surface applied litter as it is from incorporated litter (Figure 1.7). It does, however, accurately predict loss of native SOM when no substrate is added (Figure 1.8). For these reasons, I chose to alter substrate availability as a function of WFPS. Using data for respiration from the higher clay content soil, I estimated equations to predict respiration rates as a function of %WFPS. The equations are

KMC1=20000*WFPS
KMC2=332*WFPS
KMC4=667*WFPS

Rate reduction

Element ratios for the microbial biomass were allowed to float between designated values (CNMIN=5, CNMAX=20). If the ratio reached either extreme, uptake rates of all pools were set to 0. If the microbial C/N ratio exceeds 10 (CN3), the system is N limited, so the rate of C uptake is reduced linearly (up to CNMAX) depending on the exact C/N ratio. The code looks like

```
IF (CN3 .GT. CNMAX/2) THEN
RATEN=RATE*2*(CNMAX-CN3/CNMAX)
```

A similar mechanism is used to reduce the rate of nitrogen uptake when microbial C/N ratio goes below 10. The system becomes C limited, so the rate of inorganic N uptake (N6TON3) decreases by

IF (CN3 .LE. CNMIN*2) THEN
RATEN1=(CN3-CNMIN/CNMIN)*N6TON3

MODEL CALIBRATION

The microbial uptake of structural plant carbon, metabolic plant carbon and labile SOC drives the dynamics of this model. This is especially true when substrate has a low C/N ratio. These three flows are controlled by the V_{max} and the KMC of the M-M uptake expressions. The values for these parameters were estimated by fitting simulated respiration rates to rates of C loss from the fine texture soil at -0.012 MPa. Yield coefficients used in the model were taken from other studies of SOM dynamics (McGill et al. 1981; Hunt et al. 1987; van Veen et al. 1985). They were assumed to stay constant throughout the incubation. The rate of utilization of labile SOC and metabolic plant C is equal. As discussed earlier in the chapter, the flow of N is linked to C throughout the model. Phosphorus movement between certain pools is independent of C flux. Carbon uptake by the microbial biomass drives the remaining dynamics.

RESULTS and DISCUSSION

Water-filled pore space as a control on decomposition

Water-filled pore space (%WFPS) controls decomposition in the model by altering substrate availability to microorganisms. There are three sources of substrate C: metabolic plant C, structural plant C and native (SOC). Utilization of these substrates is regulated with a source-sink M-M

rate equation. Initially, %WFPS controlled the uptake of all three pools. However, when the model data were compared to the experimental data, there was poor agreement between predicted and observed results during the first 20 d of the incubation. During this period, metabolic plant C is the primary substrate for microbial growth. When litter is placed on the surface, %WFPS in the soil is likely to have little impact on microbes decomposing the surface litter. By removing the control on the uptake of metabolic plant C, experimental data matched simulated results more closely (Figure 2.2). The best fit was obtained when %WFPS regulated uptake of structural plant C and native SOC.

Given this structure for control by %WFPS, I wanted to compare experimental results for respired native SOC with and without substrate addition. Simulated results for respired native SOC after substrate addition correlated closely to experimental results (Figure 2.3). When no substrate C was added, there was little correlation between experimental and simulated results, especially at low %WFPS values (Figure 2.4). The model over-predicts the mineralization of SOC when no substrate is provided. Results from Chapter 1 suggest a strong correlation between %WFPS and mineralization of native SOC when substrate is added. This suggests that a relationship exists between SOC mineralization and %WFPS when no substrate is added. Model results suggest this is not the case, or else the model inadequately represents the process. The uptake of SOC is slower

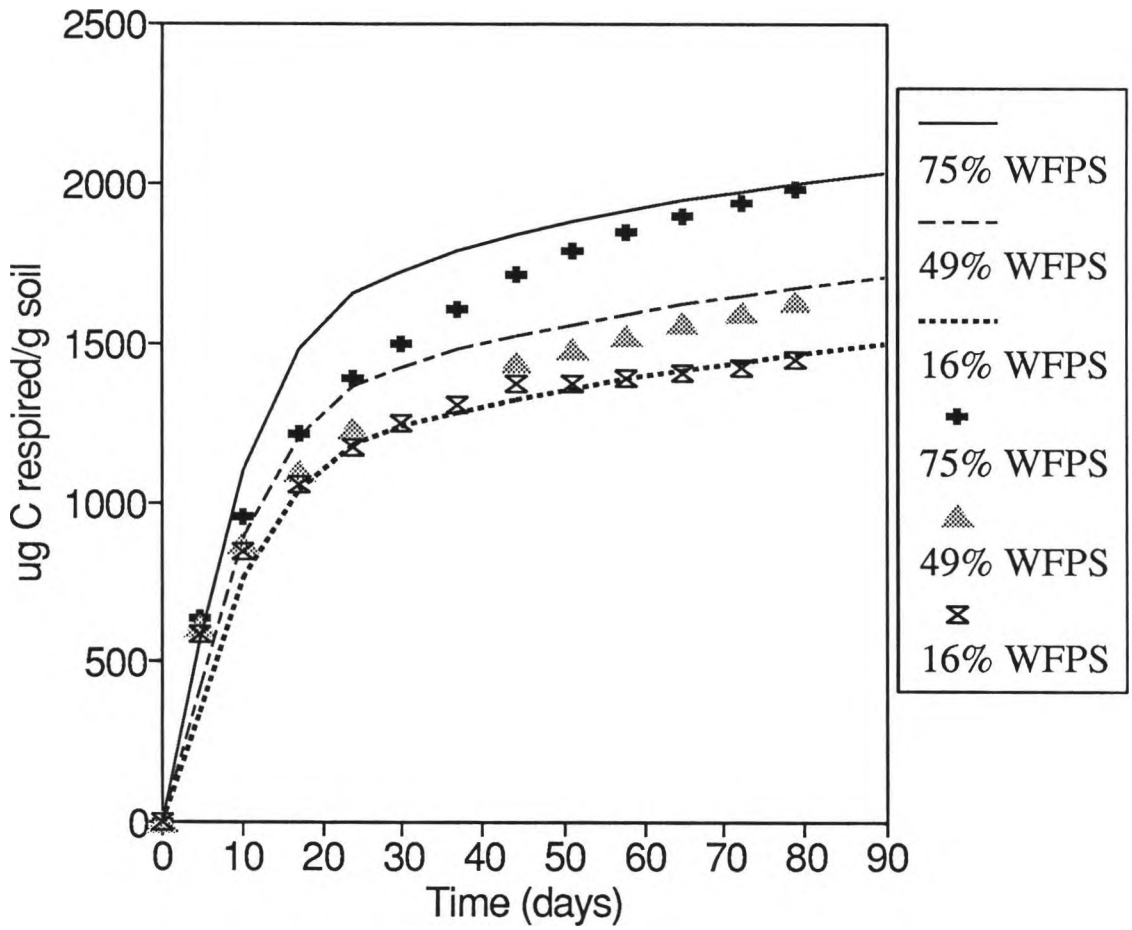

Figure 2.2. Total respiration at 3 levels of percent water-filled pore space
Experimental data shown with the symbols, simulated data represented by lines.

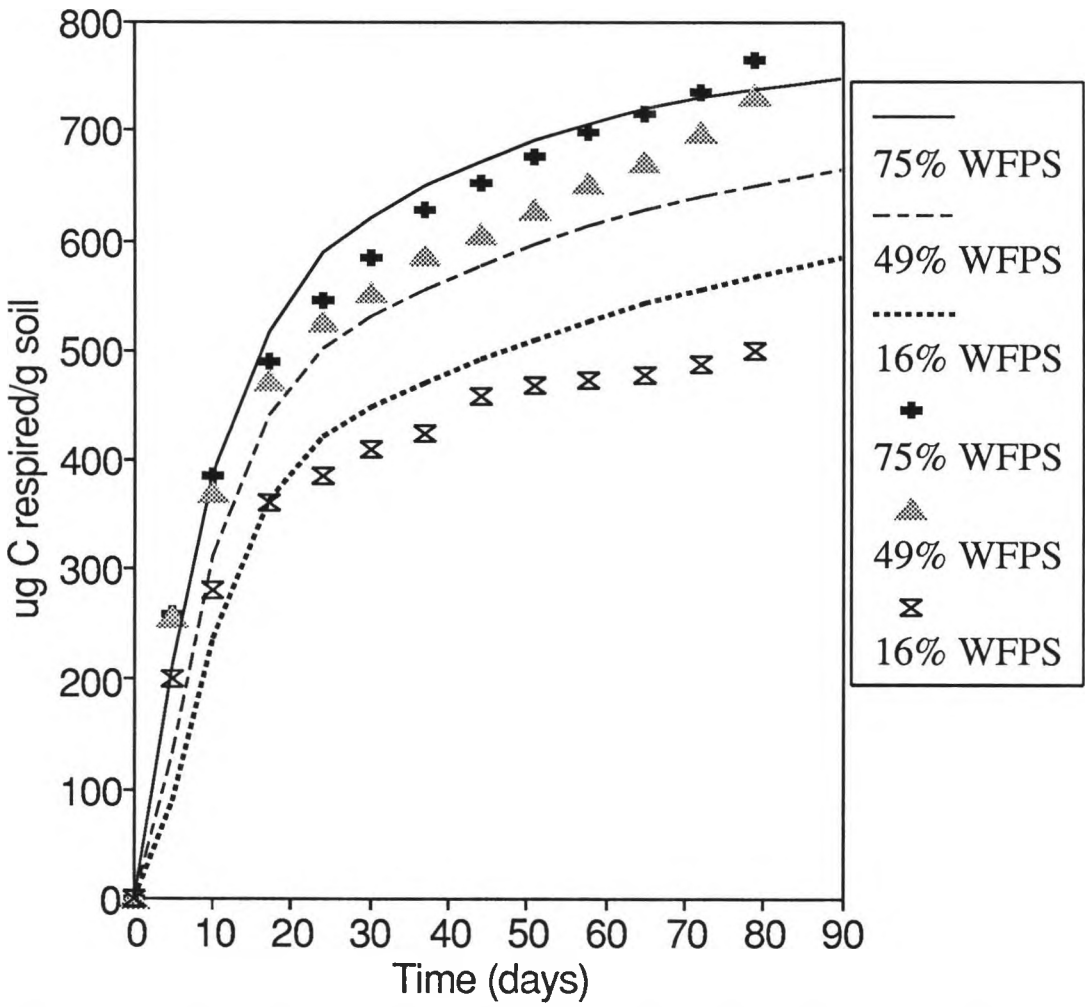

Figure 2.3. Respiration of native soil organic matter when substrate is added. Experimental data shown with symbols, simulated data represented by lines.

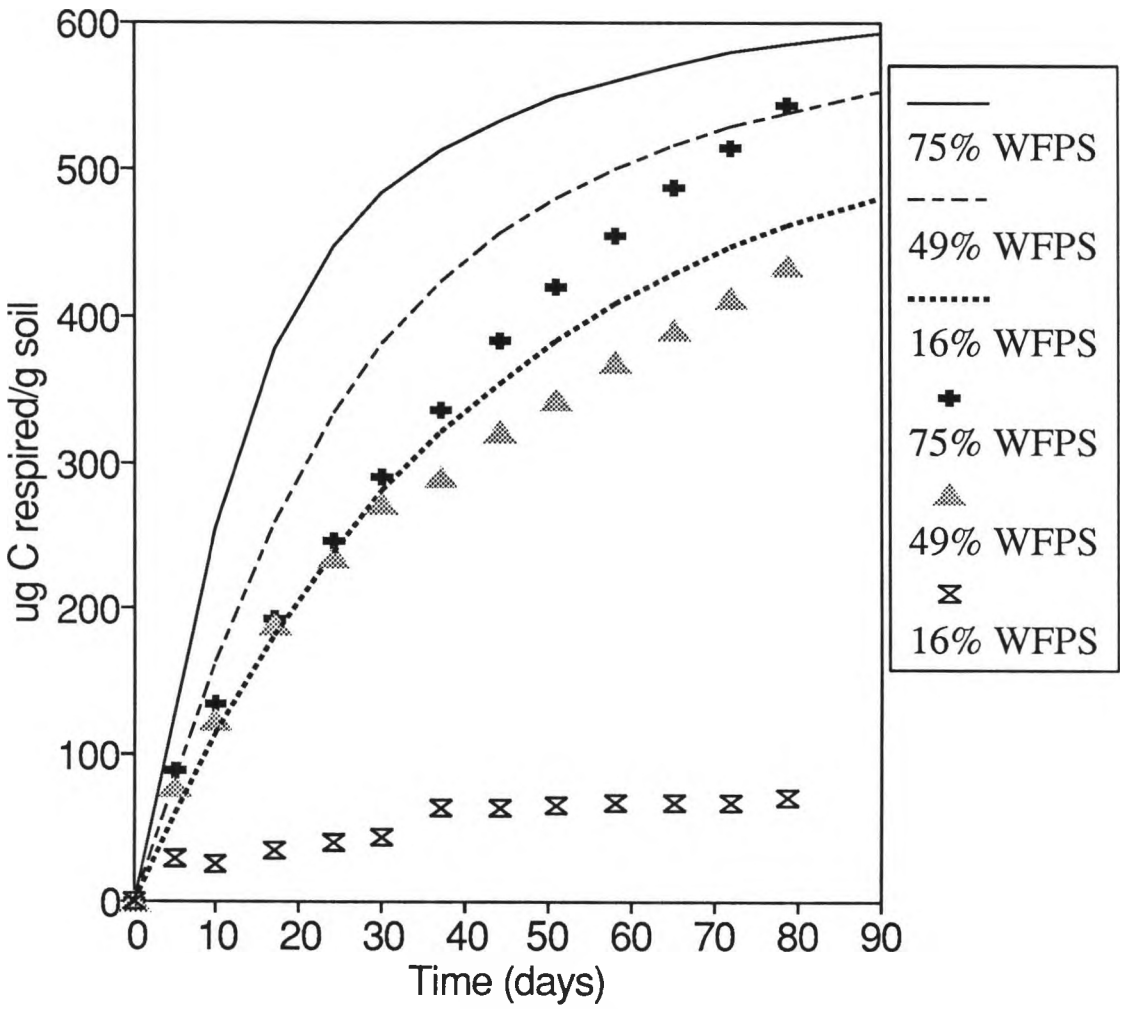

Figure 2.4. Respiration from control at 3 levels of %WFPS. Data points are shown with symbols, simulated values are shown by the lines.

when no substrate is added (Figure 2.4), suggesting that substrate addition does stimulate mineralization of SOC as shown in Chapter 1.

Effect of variability in substrate quality

This model was calibrated using data from the decomposition of plant litter with a low C/N ratio (19). The result of this calibration showed that mineral-N or mineral-P addition did not alter decomposition rate because there was adequate N and P in the litter to sustain microbial growth. This was especially apparent during the initial decay of metabolic plant C (C/N=8 in the model). Because of the low C/N ratio, the metabolic C pool comprised 40% of the total added plant C. When plant litter has a higher C/N ratio, N and maybe P availability can control the rate of decomposition (MacKay et al. 1987; McClaugherty et al. 1985). Could a model constructed for a system with no nutrient limitation and a large input of metabolic plant C show the effects of nutrient limitation at higher litter C/N ratios? Would the addition of mineral-N overcome nitrogen limitation when litter has a high C/N ratio?

Figure 2.5 shows that the model was not very sensitive to N availability as a control on total respiration. Even with the addition of 100 mg kg^{-1} inorganic N and litter with a C/N ratio of 74, respiration rates could not be elevated above those obtained when litter C/N=19 (Figure 2.5). It appears the system was either C limited or that mineral N uptake was too slow. Increased rates of N uptake had little effect on total respiration, so C limitation appears to be the limiting factor. For high C/N ratio substrates, there is very little metabolic C present (as predicted by the model). The two

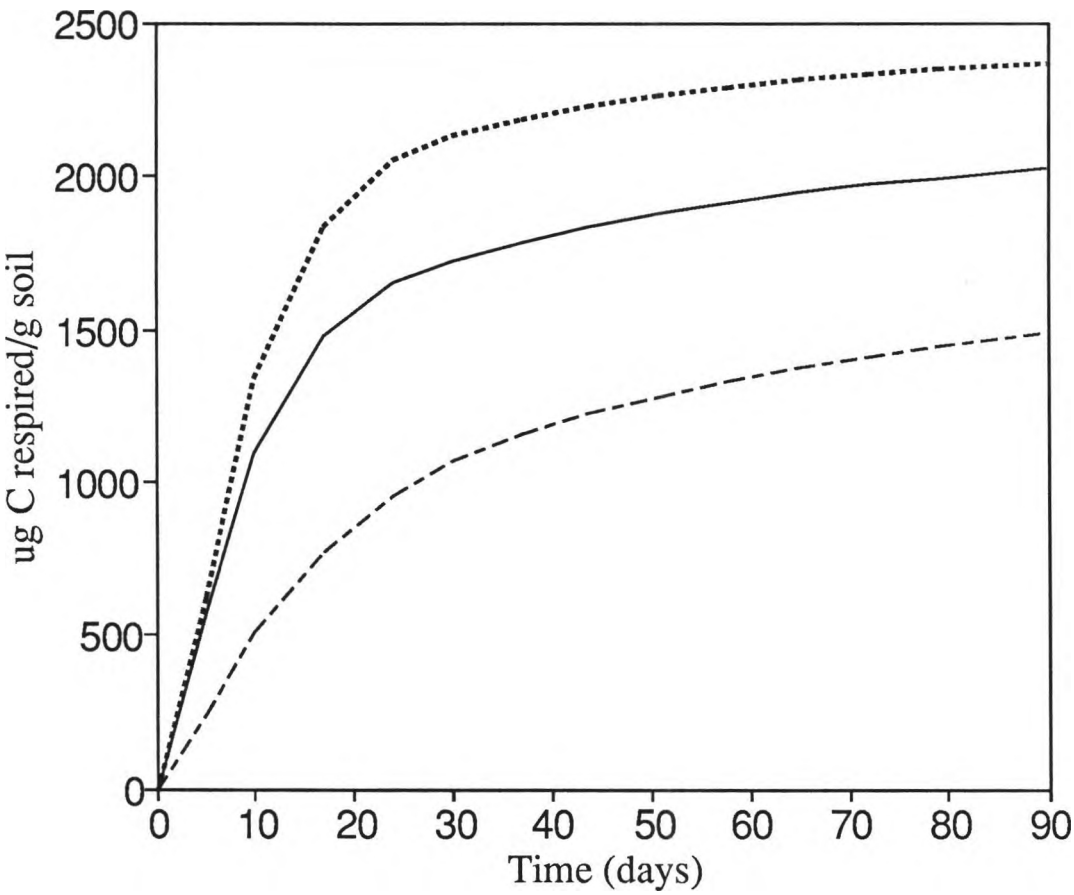

Figure 2.5: Simulated total respiration during incubation.

——— C/N ratio of added substrate=19, no mineral-N added.

– – – – – C/N ratio of added substrate=74, 100 ppm mineral-N added, same uptake parameters

····· C/N ratio of added substrate=74, 100 ppm mineral-N added, different uptake parameters.

remaining C pools are structural plant C and native SOC. It seems unlikely that addition of a higher C/N substrate further stimulates native SOC mineralization, leaving uptake of structural plant C as the only place to increase C uptake. Increasing the V_{max} of the Michaelis-Menten uptake expression for structural plant C from 1 to 5 drastically increased microbial activity, N immobilization and structural C uptake (Figures 2.5, 2.6, 2.7 and 2.8). In a peripheral experiment under identical conditions to those described in Chapter 1, decomposing litter with C/N=74 had higher total respiration during the initial 30 d of the incubation as compared to respiration rates when substrate C/N=19 (Steve Huffman **personal communication**). This result was observed only after mineral-N addition (50 mg kg^{-1}). It is reasonable, then, that simulated rates of total respiration are higher with a lower quality plant litter (Figure 2.5).

Why would utilization of structural plant C be faster when the litter has a higher C/N ratio? Microorganisms specialize on different substrates (Paul and Clark, 1989). When there is a large metabolic component to the plant litter, it is possible that groups of organisms utilizing that substrate out-compete microbes that utilize structural plant C. When this competition is removed (no metabolic C present), microbes are able to utilize the structural plant C at a fairly high rate. The model shows that about 85% of the structural plant C is used by 20 d. This is in contrast to the 25% utilized when the substrate C/N ratio=19 (Figure 2.8). This is an

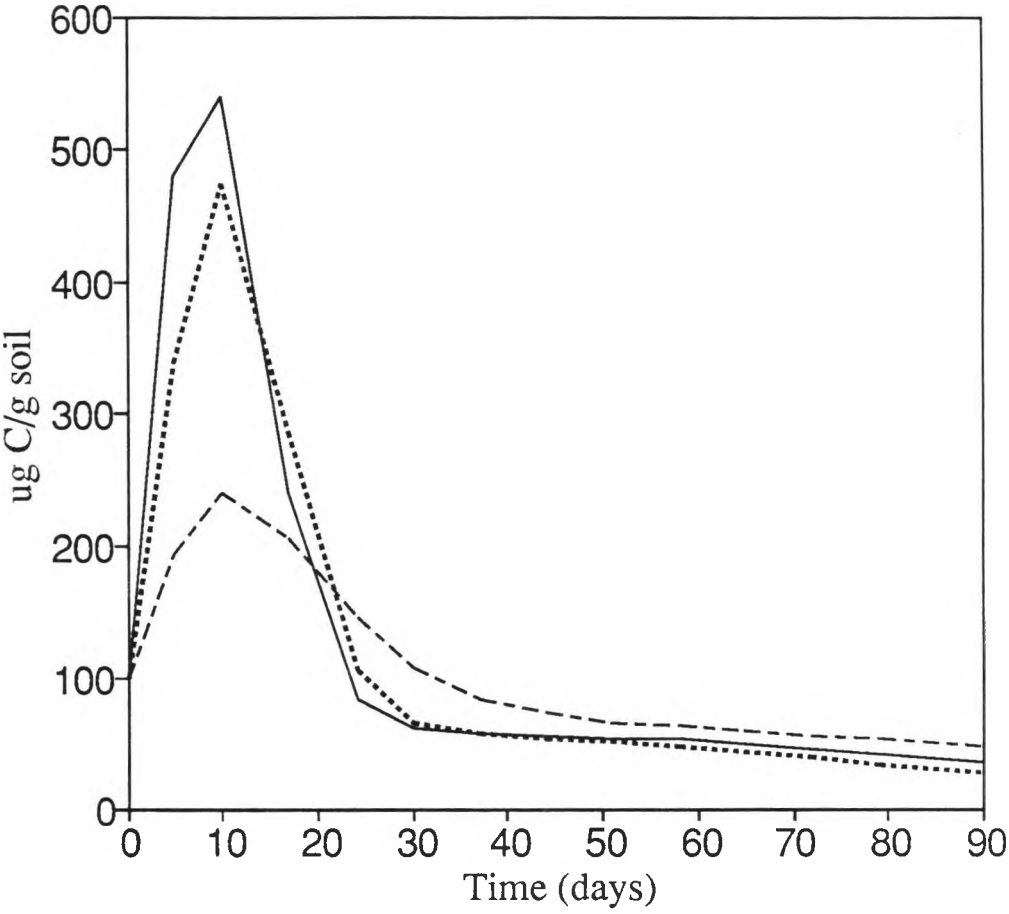

Figure 2.6: Simulated microbial biomass dynamics during incubation.

——— C/N ratio of added substrate=19, no mineral-N added.

– – – – C/N ratio of added substrate=74, 100 ppm mineral-N added, same uptake parameters

····· C/N ratio of added substrate=74, 100 ppm mineral-N added, different uptake parameters.

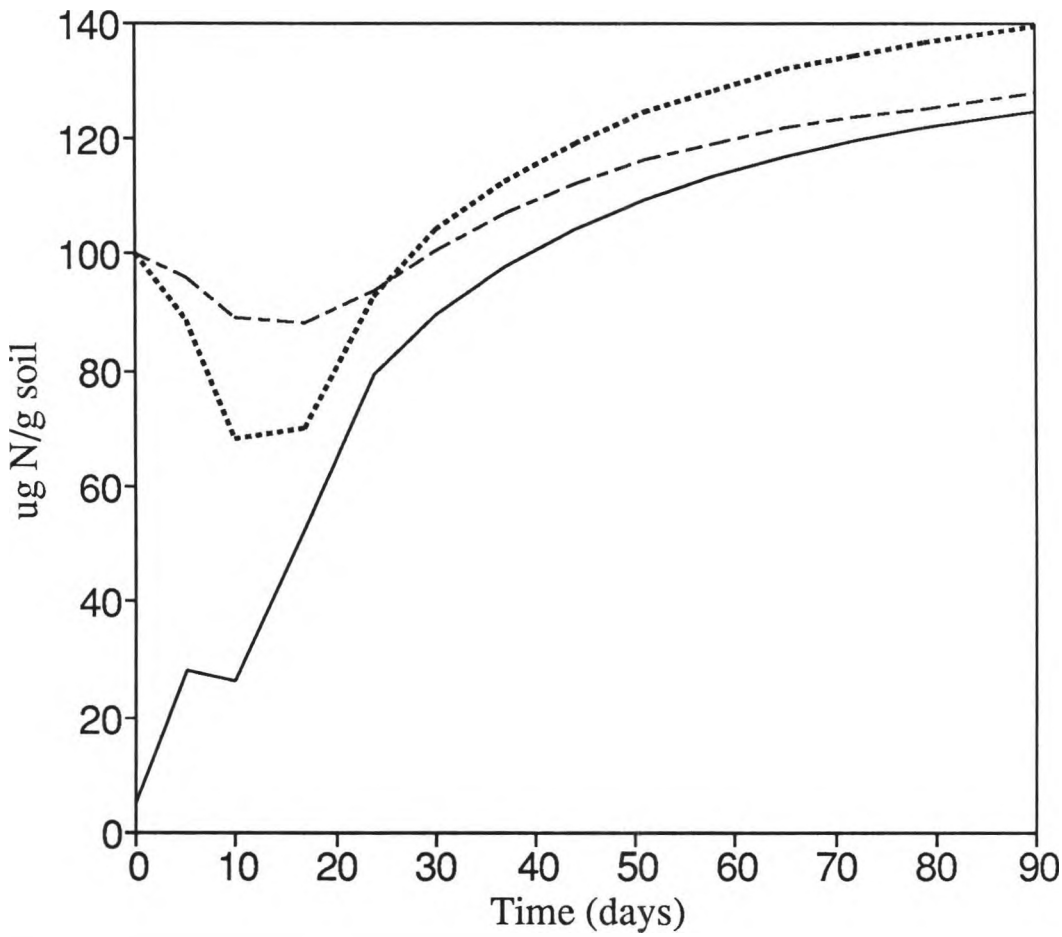

Figure 2.7: Simulated mineral nitrogen dynamics during incubation

——— C/N ratio of added substrate=19, no mineral-N added.

– – – – C/N ratio of added substrate=74, 100 ppm mineral-N added, same uptake parameters

····· C/N ratio of added substrate=74, 100 ppm mineral-N added, different uptake parameters.

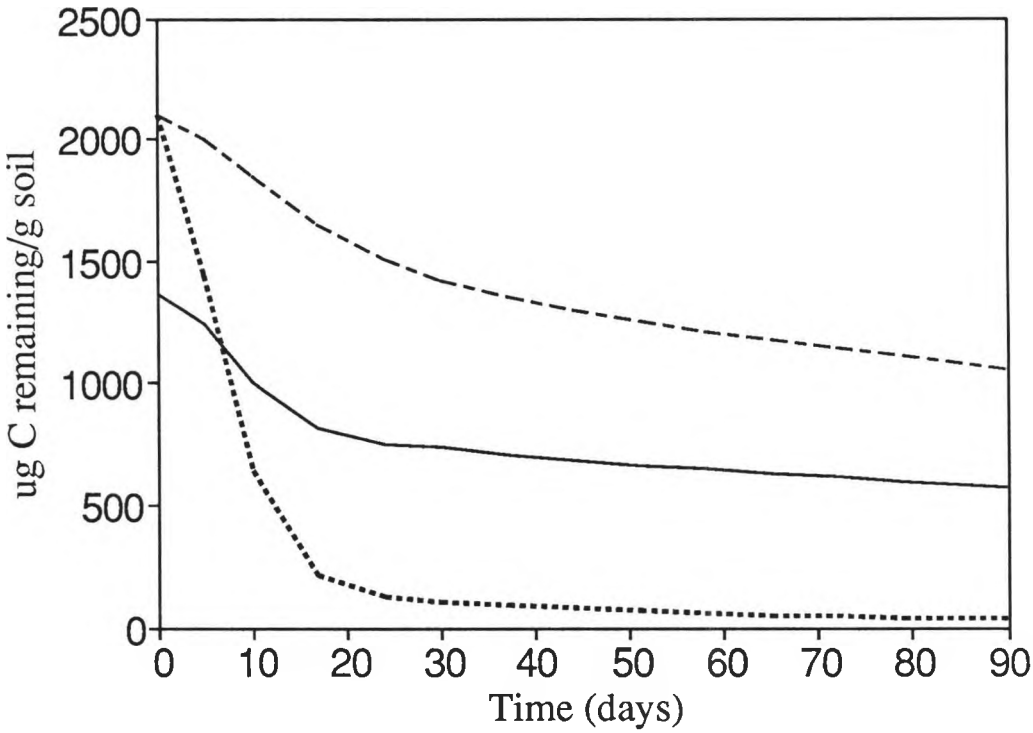

Figure 2.8: Simulated utilization of structural plant carbon during incubation.

——— C/N ratio of added substrate=19, no mineral-N added.

– – – – C/N ratio of added substrate=74, 100 ppm mineral-N added, same uptake parameters

····· C/N ratio of added substrate=74, 100 ppm mineral-N added, different uptake parameters.

interesting prediction of the model, that high quality litter decomposes slower than low quality litter when N and P supply is adequate.

CONCLUSIONS

The model presented in this chapter represents a hypothesis about mechanisms that control short-term decomposition of different quality substrates. The model was constructed based on the results described in Chapter I. This may have restricted the generality of the model to some extent, but part of the objective was to see whether a model incorporating certain processes and controls was a reasonable representation of the system across a range of initial conditions. One example of a specific process usually excluded from decomposition models is the effect of substrate addition on SOM mineralization (positive effect is called soil priming). Results from Chapter 1 indicate that this is an important process under certain conditions. The long-term formation of SOM may be controlled in part by the mineralization of native SOM resulting from substrate addition. When no substrate was added to the system, the model over-predicted respiration rates, especially in the coarse textured soil. The way this process was represented seemed to bias the system towards higher respiration rates when no substrate was added. Why a priming effect occurs under certain conditions is not well understood. Even without substrate addition, the model continued to predict extensive SOM mineralization. Somehow, the specific effect of substrate addition needs to

be represented in a different manner so that it is turned off when no substrate is added.

The use of a single driving variable that integrates the effects of soil texture and soil moisture (%WFPS) greatly simplifies how these important controls are incorporated into decomposition models. The relationship between %WFPS and respiration rate was independent of soil texture. It would be interesting to see if the relationship between respiration and %WFPS would hold if the bulk density varied with soil type (for the experiment in Chapter I, bulk density did not vary with soil type). There are several possible mechanisms by which %WFPS can influence decomposition and SOM dynamics. In this model, %WFPS controls substrate availability. This may not be the best mechanism across all conditions, but this remains to be tested.

The division of plant C into structural and metabolic fractions in the model influenced heavily respiration rate. When litter C/N was low (19), there was adequate N and P in the system (litter plus soil) so that litter decomposition was not limited by nutrient availability. However, when litter C/N was high (74), nutrient addition did not enhance litter decay rate. There is either a problem with microbial nutrient uptake in the model or the initial assignment of structural and metabolic litter C is incorrect. I found that increasing N uptake rate had little effect on litter decay (litter C/N=74). The only way to simulate faster decay of higher C/N substrate was to change the utilization of structural litter C. I could not determine

the contribution of mineralized SOM to total respiration when litter C/N=74. It is possible that litter C/N effects the magnitude of soil priming. This question requires further research. The other possible explanation for the failure of the model to simulate the decay of low quality litter is the division of litter C into structural and metabolic fractions. The C/N ratio may not be the best criteria for making this division. When litter C/N=74, there was almost no metabolic litter C, which explains why the model predicted slower decay of this material.

As a tool, the model was useful because it provided a means for testing ideas about short-term controls on litter decomposition and SOM dynamics. It also exposed several areas where my interpretation of results needed to be re-examined. In this sense, the model was very useful. I do not think it is a perfect representation of a complex process, simply a hypothesis. The model was also useful for pointing out differences in short- and long-term controls on decomposition and SOM dynamics. Used in this manner, simulation models are helpful tools for clarifying mechanisms of control that cannot be determined empirically.

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APPENDIX 1

TIME ZERO KEYSTROKE FILE FOR SIMULATION MODEL

```
"FOR"
 1 , 0 , 0 , 0 , 0 , 0 , 0 , 0 , 0 , 0 , 0 , 1 , 1 , 1 , 0 , 0 , 0 , 0 , 0 , 0
RK4
Runge-Kutta method of order 4
 2
TIME
TEND
DTPL
5
> UINITL
C
C.....SETTING LOCAL VARIABLES TO REAL
C
      REAL RATE,RATEN,RATEP
      REAL C0TOC4,C0TOC6,C1TOC5,C1TOC3,C3TOC0,CGRAZ,CGTOC4
      REAL C4TOC3,C5TOC3,C3TOC4,C3TOC6,C2TOC3,CGTOC6,C3TOC5
      REAL XC0TO4,XC0TO6,XC1TO5,XC1TO3,XC3TO0,XCGRAZ,XCGTO4
      REAL XC4TO3,XC5TO3,XC3TO4,XC3TO6,XC2TO3,XCGTO6,XC3TO5
      REAL P0TOP4,P0TOP7,P1TOP3,P1TOP5,PATOP7,P2TOP3,P3TOP0
      REAL P7TOP3,P3TOP7,P6TOP7,P7TOP6,P7TOP8,P8TOP7
      REAL P3TOP4,P3TOP5,P5TOP7,P4TOP7,P7TOP9,P9TOP7
      REAL PGRAZ,PGTOP4,PGTOP7
      REAL A3TON6,A3TON4,A3TON0,AGRAZ,AGTON4,AGTON6,A0TON6
      REAL A4TON3,A0TON4,A1TON3,A1TON5,A2TON3,A6TON3,A5TON3
      REAL A3TON5,AATON6
C
C
C.....SETTING THE INITIAL SIZE OF STRUCTURAL AND METABOLIC C
C      POOLS ON THE BASIS OF C/N RATIO IN THE RESIDUE, THE
C      C/N RATIO EXPECTED IN THE STRUCTURAL AND METABOLIC POOLS
C      AND THE QUANTITY OF RESIDUE
C
      C1 = RESC * (STCN - (MECN * STCN/RESCN))/(STCN - MECN)
      C2 = RESC - C1
       XC1=C1*SAC1
       XC2=C2*SAC2
C
C
C
C
C.....SETTING THE INITIAL SIZE OF THE STRUCTURAL AND METABOLIC
C      N POOLS
```

```
C
      N1 = C1 / STCN
      N2 = RESC/RESCN - N1 - NA
C
C
C
C.....SETTING THE INITIAL SIZE OF THE STRUCTURAL AND METABOLIC
C      P POOLS AND RESIDUE PI POOL ON THE BASIS OF THE QUANTITY
OF RESIDUE,
C      RESIDUE C/P, THE STRUCTURAL C/P AND RESIDUE C/PI RATIO.
C
      P1 = C1/STCP
      P2 = RESC/RESCP-P1-PA
C
C
C
C.....INITIAL N AND P IN GRAZER BIOMASS
C
      N0=C0/CN0
      P0=C0/CP0
C
C
C
C.....SETTING INITIAL VALUES FOR TOTAL C,N,P
C
      SUMC = C0+C1+C2+C3+C4+C5+C6
       XSUMC=XC1+XC0+XC2+XC3+XC4+XC5+XC6
      SUMN = N0+N1+N2+N3+N4+N5+N6
      SUMP = P0+P1+P2+P3+P4+P5+P6+P7+P8+P9+PA
      CN3 = C3/N3
      CP3 = C3/P3
      SOMCN = (C0+C3+C4+C5)/(N0+N3+N4+N5)
      SOMCP = (C0+C3+C4+C5)/(P0+P3+P4+P5)
      KMC1=60000*(1-WFPS)
      KMC4=2000*(1-WFPS)
.END
>UCYCL1
C
C.....DEFINE COMMON BLOCKS FOR LOCAL VARIABLES
C
      COMMON/EXTRA/RATE,RATEN,RATEP

COMMON/CAR1/C0TOC4,C0TOC6,C1TOC5,C1TOC3,C3TOC0,CGRAZ,C3TOC5

COMMON/CAR2/C4TOC3,C5TOC3,C3TOC4,C3TOC6,C2TOC3,CGTOC4,CGTOC6

COMMON/XCAR1/XC0TO4,XC0TO6,XC1TO5,XC1TO3,XC3TO0,XCGRAZ,XCGTO4
```

```
      COMMON/XCAR2/XC4TO3,XC5TO3,XC3TO4,XC3TO6,XC2TO3,XCGTO6,XC3TO5

      COMMON/PHO1/P0TOP4,P0TOP7,P1TOP3,P1TOP5,PATOP7,P2TOP3,P3TOP0
           COMMON/PHO2/P7TOP3,P3TOP7,P6TOP7,P7TOP6,P7TOP8,P8TOP7
           COMMON/PHO3/P3TOP4,P3TOP5,P5TOP7,P4TOP7,P7TOP9,P9TOP7
           COMMON/PHO4/PGRAZ,PGTOP4,PGTOP7
           COMMON/NIT1/A3TON6,A3TON4,A3TON0,AGRAZ,AGTON4
           COMMON/NIT2/AGTON6,A0TON6,A3TON5,A0TON4,A1TON3
           COMMON/NIT3/A1TON5,A2TON3,A6TON3,A5TON3,A4TON3,AATON6
C
C
C
C.....CALCULATE C/N AND C/P RATIOS FOR MICROBIAL BIOMASS (CN3,CP3)
C      AND SOIL ORGANIC MATTER (SOMCN,SOMCP)
C
           CN3 = C3/N3
           CP3 = C3/P3
           SOMCN = (C0+C3+C4+C5)/(N0+N3+N4+N5)
           SOMCP = (C0+C3+C4+C5)/(P0+P3+P4+P5)
C
C
C
C
C
C.....CARBON FLOWS
C
C
C
C.....C1TOC3   STRUCTURAL C TO MICROBIAL C
C
C              THE SUBROUTINE REDUCT IS CALLED TO DETERMINE N
C              AND P LIMITATION ON RESIDUE DECOMPOSITION
C
           RATE = C3 * C1 * VMC1 * 1/(C1 + KMC1)
           CALL REDUCT(CN3,CP3,CNMAX,CPMAX,RATE,RATEN,RATEP)
           C1TOC3 = RATE
            IF (C1 .EQ. 0) THEN
            XC1TO3=0
            ELSE
            XC1TO3=RATE * (XC1/C1)
            ENDIF
C
C
C
C.....C1TOC5   STRUCTURAL C TO STABLE C
C
           C1TOC5 = STABC * C1TOC3
            XC1TO5=STABC*XC1TO3
```

```
C
C
C
C.....C2TOC3   METABOLIC C TO MICROBIAL C
C
      RATE = C3 * C2 * VMC2 * 1/(C2 + KMC2)
      CALL REDUCT(CN3,CP3,CNMAX,CPMAX,RATE,RATEN,RATEP)
      C2TOC3 = RATE
       IF (C2 .EQ. 0) THEN
       XC2TO3=0
       ELSE
       XC2TO3=RATE*XC2/C2
       ENDIF
C
C
C.....C4TOC3   LABILE C TO MICROBIAL C
C
       RATE = C3 * C4 * VMC4 * 1/(C4 + KMC4)
      CALL REDUCT(CN3,CP3,CNMAX,CPMAX,RATE,RATEN,RATEP)
      C4TOC3 = RATE
       XC4TO3=RATE*XC4/C4
C
C
C.....C5TOC3   STABLE C TO MICROBIAL C
C
C
      RATE = C5 * KC53
      CALL REDUCT(CN3,CP3,CNMAX,CPMAX,RATE,RATEN,RATEP)
      C5TOC3 = RATE
       XC5TO3=C5TOC3*XC5/C5
C
C
C
C.....C3TOC4   MICROBIAL C TO LABILE C
C
      C3TOC4 = C3 * KC34
       XC3TO4=C3TOC4*XC3/C3
C
C.....C3TOC5  STABILIZATION OF SOME OF THE MICROBIAL METABOLITES
C
      C3TOC5 = STABZ*C3TOC4
       XC3TO5=STABZ*XC3TO4
      C3TOC4 = C3TOC4 - C3TOC5
       XC3TO4 = XC3TO4 - XC3TO5
C
C
C.....C3TOC6   MICROBIAL C TO CO2
C
```

```
      C3TOC6 = C3 * KC36
       XC3TO6=C3TOC6*XC3/C3
C
C
C
C.....C3TOC0   MICROBIAL C TO GRAZER C
C
C             THERE IS NO FLOW C3TOCO IF C3 IS LESS THAN
C             THE PHYSICALLY PROTECTED MICROBIAL BIOMASS (PROTM)
C
      C3TOC0 = C0*(C3-PROTM)*VMC3*1/(C3-PROTM+KMC3)
      IF (C3.LE.PROTM) C3TOC0=0
       IF (C3TOC0 .EQ. 0) THEN
       XC3TO0=0
       ELSE
       XC3TO0=C3TOC0*XC3/C3
       ENDIF
C
C
C
C.....C0TOC6   GRAZER C TO CO2
C
C             PROTG IS THE GRAZER BIOMASS AT WHICH GRAZERS ARE
C             DORMANT.
C
      C0TOC6=C0*KC06
      IF (C0.LE.PROTG)C0TOC6=0
       IF (C0TOC6 .EQ. 0) THEN
       XC0TO6=0
       ELSE
       XC0TO6 = C0TOC6*XC0/C0
       ENDIF
C
C
C
C.....C0TOC4    GRAZER C TO LABILE ORGANIC C
C
      C0TOC4=C0*KC04
      IF (C0.LE.PROTG) C0TOC4=0
       IF (C0TOC4 .EQ. 0) THEN
       XC0TO4=0
       ELSE
       XC0TO4 = C0TOC4*XC0/C0
       ENDIF
C
C
C
C.....CGTOC4    CARBON THAT FLOWS THROUGH GRAZERS TO LABILE
```

```
C               ORGANIC CARBON
C               PART IS THE PARTION FACTOR INTO LABILE
C               ORGANIC C
C
      CGTOC4=(1-YC30)*C3TOC0*PART
       XCGTO4 = CGTOC4*XC3/C3
C
C
C
C.....NITROGEN FLOWS
C
C.....AATON6    RESIDUE NI TO INORGANIC N
C
      AATON6=NA
C
C
C
C.....A3TON6    MICROBIAL N TO MINERAL N
C
      A3TON6 = C3TOC6 * N3/C3
C
C
C
C.....A3TON4    MICROBIAL N TO LABILE ORGANIC N
C
      A3TON4 = C3TOC4 * N3/C3
C
C
C
C.....A3TON0    MICROBIAL N TO GRAZER N
C
      A3TON0=C3TOC0*N3/C3
C
C
C
C.....AGRAZ     NITROGEN THAT IS RETAINED IN GRAZER BIOMASS
C
      AGRAZ=YC30*C3TOC0/CN0
C
C
C.....AGTON4    NITROGEN THAT FLOWS THROUGH GRAZER BIOMASS TO
C               LABILE ORGANIC N
C
      AGTON4=CGTOC4*N3/C3*F4CN3
C
C
C
C.....AGTON6     NITROGEN THAT FLOWS THROUGH GRAZER BIOMASS TO
```

```
C               MINERAL N
C
      AGTON6=A3TON0-AGRAZ-AGTON4
C
C
C
C.....A0TON6    GRAZER N TO MINERAL N COUPLED TO GRAZER
C               RESPIRATION
C
      A0TON6=C0TOC6/CN0
C
C
C
C.....A0TON4    GRAZER N TO LABILE ORGANIC N
C
      A0TON4=C0TOC4/CN0
C
C
C
C.....A1TON3    STRUCTURAL N TO MICROBIAL N
C
      IF (C1 .LE. 0) THEN
        A1TON3 = 0
      ELSE
        A1TON3 = C1TOC3 * N1/C1
      END IF
C
C
C
C.....A1TON5    STRUCTURAL N TO STABLE ORGANIC N
C
      IF (C1 .LE. 0) THEN
        A1TON5 = 0
      ELSE
        A1TON5 = C1TOC5 * N1/C1
      END IF
C
C
C
C.....A2TON3    METABOLIC N TO MICROBIAL N
C
      IF (C2 .LE. 0) THEN
        A2TON3 = 0
      ELSE
        A2TON3 = C2TOC3 * N2/C2
      END IF
C
C
```

```
C
C.....A6TON3    MINERAL N TO MICROBIAL N
C
      A6TON3 = C3 * N6 * VMN6 * 1/(KMN6 + N6)
C
C
C
C.....RATE LIMITING STEP WHEN CN3 IS TOO LOW. C LIMITATION
C
      IF (CN3 .LE. CNMIN*2) A6TON3 = (CN3-CNMIN)/CNMIN * A6TON3
      IF (CN3 .LE. CNMIN) A6TON3=0
C
C
C
C.....A5TON3    STABLE N TO MICROBIAL N
C
      A5TON3=C5TOC3*N5/C5
C
C
C
C.....A4TON3    LABILE N TO MICROBIAL N
C
      IF (C4 .LE. 0) THEN
        A4TON3 = 0
      ELSE
        A4TON3=C4TOC3*N4/C4
      END IF
C
C
C
C.....A3TON5    MICROBIAL N TO STABLE ORGANIC N
C
      A3TON5=C3TOC5*N3/C3*F5CN3
C
C
C
C
C.....PHOSPHORUS FLOWS
C
C
C
C.....PATOP7    RESIDUE PI TO LABILE PI
C
      PATOP7=PA
C
C
C
C.....P1TOP3    STRUCTURAL P TO MICROBIAL P
```

```
C
      IF (C1 .LE. 0) THEN
        P1TOP3 = 0
      ELSE
        P1TOP3 = C1TOC3 * P1/C1
      END IF
C
C
C
C.....P1TOP5    STRUCTURAL P TO STABLE ORGANIC P
C
      IF (C1 .LE. 0) THEN
        P1TOP5 = 0
      ELSE
        P1TOP5 = C1TOC5 * P1/C1
      END IF
C
C
C
C.....P2TOP3    METABOLIC P TO MICROBIAL P
C
      IF (C2 .LE. 0) THEN
        P2TOP3 = 0
      ELSE
        P2TOP3 = C2TOC3 * P2/C2
      END IF
C
C
C
C.....P7TOP3    LABILE P TO MICROBIAL P DEPENDENT ON WATER
SOLUBLE
C               P CONCENTRATION
C
      P7TOP3=C3*P6* VMP6 * 1/(KMP6 + P6)
C
C
C
C..... MINERALIZATION OF SOIL ORGANIC P THROUGH PHOSPHATASE
ACTIVITY
C
      SPASE=(A1*EXP(B1*P6))*KSP
      MPASE=A/(1+B*EXP(-C*CP3))
C
C
C.....P4TOP7    LABILE ORGANIC P TO LABILE PI
C
         P4TOP7=(P4*SPASE+P4*C3*MPASE)*KP47
C
```

```
C..... P5TOP7    STABLE ORGANIC P TO LABILE PI
C
        P5TOP7=(P5*SPASE+P5*C3*MPASE)*KP57
C
C
C
C
C.....P3TOP7    MICROBIAL P TO LABILE P
C
     P3TOP7=P3/C3 * C3TOC6
C
C
C
C.....P6TOP7    WATER SOLUBLE P TO LABILE PI
C
     P6TOP7=P6*KP67
C
C
C
C.....P7TOP6    LABILE PI TO WATER SOLUBLE P
C
     P7TOP6=P7*KP76
C
C
C
C.....P7TOP8    LABILE PI TO NAOH EXTRACTABLE PI DEPENDENT
C               ON WATER SOLUBLE P CONCENTRATION
C
     P7TOP8=P6*KP78
C
C
C
C.....P8TOP7    NAOH EXTRACTABLE PI TO LABILE PI
C
     P8TOP7=P8*KP87
C
C
C
C.....P3TOP0    MICROBIAL P TO GRAZER P
C
     P3TOP0=C3TOC0*P3/C3
C
C
C
C.....PGRAZ     PHOSPHORUS THAT IS RETAINED IN GRAZER BIOMASS
C
     PGRAZ=YC30*C3TOC0/CP0
C
```

```
C
C.....PGTOP4    PHOSPHORUS THAT FLOWS THROUGH GRAZER BIOMASS
TO
C               LABILE ORGANIC P(DEPENDENT ON 2 TIMES THE C:P RATIO
FOR C3)
C
      PGTOP4=CGTOC4*P3/C3*F4CP3
C
C
C
C.....PGTOP7     PHOSPHORUS THAT FLOWS THROUGH GRAZER BIOMASS
TO
C                LABILE PI
C
      PGTOP7=P3TOP0-PGRAZ-PGTOP4
C
C
C.....P0TOP7    GRAZER P TO LABILE PI COUPLED TO GRAZER
C               RESPIRATION
C
      P0TOP7=C0TOC6/CP0
C
C
C
C.....P0TOP4    GRAZER P TO LABILE ORGANIC P
C
      P0TOP4=C0TOC4/CP0
C
C
C
C.....P3TOP4    MICROBIAL P TO LABILE ORGANIC P
C
      P3TOP4=P3*KP34
C
C
C
C.....P3TOP5    MICROBIAL P TO STABLE ORGANIC P
C
      P3TOP5=C3TOC5*P3/C3*F5CP3
C
C
C
C.....P7TOP9    LABILE PI TO HCL EXTRACTABLE P DEPENDENT ON
WATER
C               SOLUBLE P CONCENTRATION
C
      P7TOP9=P6*KP79
C
```

```
C
C
C.....P9TOP7     HCL EXTRACTABLE PI TO LABILE PI
C
      P9TOP7=P9*KP97
C
C
C
C.....ELIMINATION OF THE FLOWS OF C,N AND P TO GRAZER BIOMASS
C     WHEN THE QUALITY OF THE MICROBIAL BIOMASS IS TO LOW TO
SUPPORT
C     THE GRAZERS
C
C     C3TOC0*N3/C3 IS THE TOTAL AMOUNT OF N PASSED TO GRAZERS
C     C3TOC0*P3/C3 IS THE TOTAL AMOUNT OF P PASSED TO GRAZERS
C
C     AGRAZ AND PGRAZ ARE THE AMOUNTS OF N AND P NEEDED IN THE

C     MICROBIAL BIOMASS TO MAKE IT USABLE (AND ALSO THE AMOUNT
OF N
C     AND P RETAINED BY GRAZER BIOMASS WHEN N AND P ARE IN
EXCESS)
C
C           NITROGEN AND PHOSPHORUS LIMITATION
C
      IF(C3TOC0*N3/C3.LT.AGRAZ .OR. C3TOC0*P3/C3.LT.PGRAZ) THEN
       CGTOC4=0
       C3TOC0=0
       AGTON4=0
       AGTON6=0
       A3TON0=0
       PGTOP4=0
       PGTOP7=0
       P3TOP0=0
       XCGTO4=0
       XC3TO0=0
      ELSE
      CONTINUE
      ENDIF
C
C
C
.END
>DIFFERENTIAL EQUATIONS
DERIV1
/STAT1/
/PARAM1/
DT
```

C0,
C1,
C2,
C3,
C4,
C5,
C6,
XC0,
XC1,
XC2,
XC3,
XC4,
XC5,
XC6,
SOMCO2,
XSOM,
N0,
N1,
N2,
N3,
N4,
N5,
N6,
NA,
P0,
P1,
P2,
P3,
P4,
P5,
P6,
P7,
P8,
P9,
PA,
.END
SAC1,
SAC2,
VMC1,
KMC1,
VMC2,
KMC2,
VMC3,
KMC3,
VMC4,
KMC4,
KC04,
KC06,

KC36,
KC34,
KC53,
KP34,
KP35,
KP37,
KP47,
KP57,
KP67,
KP76,
KP78,
KP87,
KP97,
KP79,
VMN6,
KMN6,
VMP6,
KMP6,
YC13,
YC23,
YC30,
YC43,
YC53,
STABC,
CNMAX,
CNMIN,
CPMAX,
STCN,
STCP,
MECN,
RESCN,
RESCP,
RESC,
PROTM,
PROTG,
CN0,
CP0,
KSP,
PART,
A,
B,
C,
A1,
B1,
STABZ,
WFPS,
F4CN3,
F5CN3,

```
F4CP3,
F5CP3,
.END
C
C
C.....DEFINE COMMON BLOCKS FOR LOCAL VARIABLES
C
C
      COMMON/EXTRA/RATE,RATEN,RATEP

COMMON/CAR1/C0TOC4,C0TOC6,C1TOC5,C1TOC3,C3TOC0,CGRAZ,C3TOC5

COMMON/CAR2/C4TOC3,C5TOC3,C3TOC4,C3TOC6,C2TOC3,CGTOC4,CGTOC6

COMMON/XCAR1/XC0TO4,XC0TO6,XC1TO5,XC1TO3,XC3TO0,XCGRAZ,XCGTO4

COMMON/XCAR2/XC4TO3,XC5TO3,XC3TO4,XC3TO6,XC2TO3,XCGTO6,XC3TO5

COMMON/PHO1/P0TOP4,P0TOP7,P1TOP3,P1TOP5,PATOP7,P2TOP3,P3TOP0
      COMMON/PHO2/P7TOP3,P3TOP7,P6TOP7,P7TOP6,P7TOP8,P8TOP7
      COMMON/PHO3/P3TOP4,P3TOP5,P5TOP7,P4TOP7,P7TOP9,P9TOP7
      COMMON/PHO4/PGRAZ,PGTOP4,PGTOP7
      COMMON/NIT1/A3TON6,A3TON4,A3TON0,AGRAZ,AGTON4
      COMMON/NIT2/AGTON6,A0TON6,A3TON5,A0TON4,A1TON3
      COMMON/NIT3/A1TON5,A2TON3,A6TON3,A5TON3,A4TON3,AATON6
C
C
      D:C0 =YC30*C3TOC0 - C0TOC6 - C0TOC4
       D:XC0=YC30*XC3TO0 - XC0TO6 - XC0TO4
      D:C1 = - C1TOC3 - C1TOC5
       D:XC1=-XC1TO3 - XC1TO5
      D:C2 = - C2TOC3
       D:XC2=-XC2TO3
      D:C3 = YC13*C1TOC3 + YC23*C2TOC3 + YC43*C4TOC3
       D:XC3 = YC13*XC1TO3+YC23*XC2TO3+YC43*XC4TO3
      D:C3 += YC53*C5TOC3 -C3TOC4 -C3TOC6-C3TOC0-C3TOC5
      D:XC3 += YC53*XC5TO3 -XC3TO4 -XC3TO6-XC3TO0-XC3TOC5
      D:C4 = C3TOC4 - C4TOC3 + C0TOC4 + CGTOC4
       D:XC4 = XC3TO4 - XC4TO3 +XC0TO4 + XCGTO4
      D:C5 = C1TOC5 - C5TOC3 + C3TOC5
      D:XC5 = XC1TO5 - XC5TO3 + XC3TO5
      D:C6 = (1-YC13)*C1TOC3 + (1-YC23)*C2TOC3 + (1-YC43)*C4TOC3
      D:C6 += (1-YC53)*C5TOC3 + C3TOC6 + C0TOC6
      D:C6 += (1-YC30)*C3TOC0 - CGTOC4
      D:XC6 = (1-YC13)*XC1TO3 + (1-YC23)*XC2TO3 + (1-YC43)*XC4TO3
      D:XC6 += (1-YC53)*XC5TO3 + XC3TO6 +XC0TO6
      D:XC6 += (1-YC30)*XC3TO0 -XCGTO4
      IC6 = (1-YC13)*C1TOC3 + (1-YC23)*C2TOC3 + (1-YC43)*C4TOC3
```

```
      IC6 += (1-YC53)*C5TOC3 + C3TOC6 + C0TOC6
      IC6 += (1-YC30)*C3TOC0 - CGTOC4
      XIC6 = (1-YC13)*XC1TO3 + (1-YC23)*XC2TO3 + (1-YC43)*XC4TO3
      XIC6 += (1-YC53)*XC5TO3 + XC3TO6 +XC0TO6
      XIC6 += (1-YC30)*XC3TO0 - XCGTO4
      RATEC4=(1-YC43)*C4TOC3 + (1-YC53)*C5TOC3
      XRATE4=(1-YC43)*XC4TO3+(1-YC53)*XC5TO3
      D:SOMCO2=(1-YC43)*C4TOC3 + (1-YC53)*C5TOC3
      D:XSOM=(1-YC43)*XC4TO3+(1-YC53)*XC5TO3
      D:N0 = A3TON0 - A0TON6 - A0TON4 - AGTON6 - AGTON4
      D:N1 = - A1TON3 - A1TON5
      D:N2 = - A2TON3
       IF (CN3 .LE. CNMIN) THEN
      D:N3=A6TON3-A3TON4-A3TON6-A3TON0
       ELSE
      D:N3 = A6TON3 + A1TON3 + A2TON3 - A3TON4 - A3TON6
      D:N3 += A4TON3 + A5TON3 - A3TON0
       ENDIF
      D:N4 = A3TON4 - A4TON3 + A0TON4 + AGTON4
      D:N5 = A1TON5 - A5TON3
       IF (CN3 .LE. CNMIN) THEN
      D:N6=A3TON6+A1TON3+A2TON3+A4TON3+A5TON3-A6TON3
      D:N6 += A0TON6 + AGTON6 + AATON6
       ELSE
      D:N6 = - A6TON3 + A3TON6 + A0TON6 + AGTON6 + AATON6
       ENDIF
      D:NA = -AATON6
      D:P0 = P3TOP0 - P0TOP7 - P0TOP4 - PGTOP4 - PGTOP7
      D:P1 = - P1TOP3 - P1TOP5
      D:P2 = - P2TOP3
      D:P3 = P1TOP3 + P2TOP3 - P3TOP4
      D:P3 += P7TOP3 - P3TOP7 - P3TOP5 - P3TOP0
      D:P4 = P3TOP4 - P4TOP7 + P0TOP4 + PGTOP4
      D:P5 = P1TOP5 + P3TOP5 - P5TOP7
      D:P6 = P7TOP6-P6TOP7
      D:P7 = P3TOP7 + P4TOP7 +P5TOP7+ P8TOP7 + P9TOP7 + P0TOP7
      D:P7 += P6TOP7 - P7TOP3 - P7TOP6 - P7TOP8 - P7TOP9
      D:P7 += PATOP7 + PGTOP7
      D:P8 = P7TOP8 - P8TOP7
      D:P9 = - P9TOP7 + P7TOP9
      D:PA = -PATOP7
.END
.END
> UCYCL2
C
C
C.....DEFINE COMMON BLOCKS FOR LOCAL VARIABLES
C
```

```
C
      COMMON/EXTRA/RATE,RATEN,RATEP

COMMON/CAR1/C0TOC4,C0TOC6,C1TOC5,C1TOC3,C3TOC0,CGRAZ,C3TOC5

COMMON/CAR2/C4TOC3,C5TOC3,C3TOC4,C3TOC6,C2TOC3,CGTOC4,CGTOC6

COMMON/XCAR1/XC0TO4,XC0TO6,XC1TO5,XC1TO3,XC3TO0,XCGRAZ,XCGTO4

COMMON/XCAR2/XC4TO3,XC5TO3,XC3TO4,XC3TO6,XC2TO3,XCGTO6,XC3TO5

COMMON/PHO1/P0TOP4,P0TOP7,P1TOP3,P1TOP5,PATOP7,P2TOP3,P3TOP0
      COMMON/PHO2/P7TOP3,P3TOP7,P6TOP7,P7TOP6,P7TOP8,P8TOP7
      COMMON/PHO3/P3TOP4,P3TOP5,P5TOP7,P4TOP7,P7TOP9,P9TOP7
      COMMON/PHO4/PGRAZ,PGTOP4,PGTOP7
      COMMON/NIT1/A3TON6,A3TON4,A3TON0,AGRAZ,AGTON4
      COMMON/NIT2/AGTON6,A0TON6,A3TON5,A0TON4,A1TON3
      COMMON/NIT3/A1TON5,A2TON3,A6TON3,A5TON3,A4TON3,AATON6
C
C       CREATE A VARIABLE THAT COMBINES GRAZERS AND MICROBES
INTO ONE
C       VARIABLE (C0C3)
C
       C0C3=C3+C0
       N0N3=N3+N0
       P0P3=P3+P0
C
C.....RATE OF CO2 PRODUCTION (MICROBIAL RESPIRATION)
C
      XRESP = XIC6
       RESP = IC6
C
C
C
C.....CHECK ON CONSERVATION OF MASS
C
      SUMC = C0+C1+C2+C3+C4+C5+C6
       XSUMC = XC0+XC1+XC2+XC3+XC4+XC5+XC6
      SUMN = N0+N1+N2+N3+N4+N5+N6
      SUMP = P0+P1+P2+P3+P4+P5+P6+P7+P8+P9+PA
C
C
C
C.....CHECK GRAZER C/N AND C/P RATIOS
C
      GCN = C0/N0
      GCP = C0/P0
C
```

```
C
.END
> SUBROUTINES
C
C.....SUBROUTINE FOR CARBON DECOMPOSITION RATE REDUCTION
C      WHEN N AND P LIMITING
C
      SUBROUTINE REDUCT(CN3,CP3,CNMAX,CPMAX,RATE,RATEN,RATEP)
C
      IF (CN3 .GT. CNMAX/2) THEN
        RATEN = RATE*2*(CNMAX-CN3)/CNMAX
      ELSE
        RATEN=RATE
      END IF
C
      IF (CN3 .GE. CNMAX) RATEN = 0
C
      IF (CP3 .GT. CPMAX/2) THEN
        RATEP = RATE*2*(CPMAX-CP3)/CPMAX
      ELSE
        RATEP=RATE
      END IF
C
      IF (CP3 .GE. CPMAX) RATEP = 0
C
      IF (RATEN .LE. RATEP) THEN
        RATE = RATEN
      ELSE
        RATE = RATEP
      END IF
      RETURN
      END
C
.END
>CHECKN
Y
S
SUMC,
XSUMC,
XRESP,
SUMN,
SUMP,
RESP,
IC6,
RATEC4,
XRATE4,
CN3,
CP3,
```

```
SOMCN,
SOMCP,
GCN,
GCP,
SPASE,
MPASE,
C0C3,
N0N3,
P0P3,
.END
N
 0 ;TIME'      is the initial value assigned to the simulated time
 15 ;C0'      grazer C
 0 ;C1'       structural C (dummy)
 0 ;C2'       metabolic C  (dummy)
 100 ;C3'      microbial C
 500 ;C4'      labile SOC
 7400 ;C5'     SLOW SOC
 0 ;C6'       CO2
 0 ;XC0
 0 ;XC1
 0 ;XC2
 0 ;XC3
 0 ;XC4
 0 ;XC5
 0 ;XC6
 0 ;SOMCO2'    SOM derived CO2
 0 ;XSOM
 0 ;N0'       grazer N
 0 ;N1'       structural N (dummy)
 0 ;N2'       metabolic N (dummy)
 10 ;N3'      microbial N
 10 ;N4'      labile organic N
 740 ;N5'     stable organic N
 5 ;N6'       mineral NO3 + NH4
 30 ;NA'      residue Ni
 0 ;P0'       grazer P
 0 ;P1'       structural P (dummy)
 0 ;P2'       metabolic P (dummy)
 7 ;P3'       microbial P
 2 ;P4'       labile organic P
 15 ;P5'      stable organic P
 1.7 ;P6'     water soluble P
 31 ;P7'      labile (resin) P
 29 ;P8'      secondary mineral P
 238 ;P9'     primary mineral P
 6.4 ;PA'     residue Pi
 0 ;SUMC'      total C (dummy)
```

0 ;XSUMC
0 ;XRESP
0 ;SUMN' total N (dummy)
0 ;SUMP' total P (dummy)
0 ;RESP' rate of CO2 production (dummy)
0 ;IC6' "
0 ;RATEC4' rate of CO2 production from SOM
0 ;XRATE4' rate of CO2 production from XSOM
0 ;CN3' microbial C/N (dummy)
0 ;CP3' microbial C/P (dummy)
0 ;SOMCN' som C/N (dummy)
0 ;SOMCP' som C/P (dummy)
0 ;GCN' grazer C/N check
0 ;GCP' grazer C/P check
0 ;SPASE' soil phosphatase activity
0 ;MPASE' microbial phosphatase activity
0 ;C0C3' C combination of microbial and grazer biomass
0 ;N0N3' N combination of microbial and grazer biomass
0 ;P0P3' P combination of microbial and grazer biomass
90 ;TEND' is the time at which a simulation will end.
1 ;DTPL' is the time step on which simulated values are stored for plotting or printing
.1 ;DT' is the time step or integration interval to be used.
10.1 ;SAC1
18 ;SAC2
1 ;VMC1' Michaelas-Menton vmax C1 to C3
15000 ;KMC1' Michaelas-Menton km C1 to C3
.7 ;VMC2' Michaelas-Menton vmax C2 to C3
300 ;KMC2' Michaelas-Menton km C2 to C3
2 ;VMC3' Michaelis-menten vmax C3 to C0
500 ;KMC3' Michaelis-menten km C3 to C0
.7 ;VMC4' Michaelas-Menton vmax C4 to C3
300 ;KMC4' Michaelas-Menton km C4 to C3
.04 ;KC04' rate constant C0 to C4
.02 ;KC06' rate constant C0 to c6
.02 ;KC36' rate constant C3 to C6
.02 ;KC34' rate constant C3 to C4
.00002 ;KC53' rate constant C5 to C3
.05 ;KP34' rate constant P3 to P4
.01 ;KP35' rate constant P3 to P5
.1 ;KP37' rate constant P3 to P7
1 ;KP47' rate constant P4 to P7
.01 ;KP57' rate constant P5 to P7
1 ;KP67' rate constant P6 to P7
.055 ;KP76' rate constant P7 to P6
.000093 ;KP78' rate constant P7 to P8
.0001 ;KP87' rate constant p8 to p7
.0001 ;KP97' rate constant p9 to p7

```
.000767 ;KP79' rate constant p7 to p9
.02 ;VMN6'    Michaelas-Menton vmax N6 to N3
5 ;KMN6'      Michaelas-Menton km N6 to N3
.02 ;VMP6'    Michaelas-Menton vmax P6 to P3
1 ;KMP6'      Michaelas-Menton km P6 to P3
.3 ;YC13'     yield C C1 to C3
.55 ;YC23'    yield C C2 to C3
.2 ;YC30'     yield C C3 to C0
.4 ;YC43'     yield C C4 to C3
.2 ;YC53'     yield C C5 to C3
.2 ;STABC'    flow from C1 to C5 relative to flow from C1 to C3
20 ;CNMAX'     microbial C/N at which rate = 0
5 ;CNMIN'     microbial C/N at which rate=0  C limitation
100 ;CPMAX'   microbial C/P at which rate = 0
100 ;STCN'    structural C/N
1000 ;STCP'   structural C/P
8 ;MECN'      metabolic C/N
19 ;RESCN'    residue C/N
220 ;RESCP'   residue C/P
2171 ;RESC'   mass residue C
50 ;PROTM'    protected microbial biomass
2 ;PROTG'     protected grazer biomass
5 ;CN0'       grazer C/N
12.5 ;CP0'    grazer C/P
.25 ;KSP'     soil phosphatase factor related to SOC
.7 ;PART'     partition of grazer C to labile organic carbon
.001 ;A'      microbial phosphatase logistic parameter
250 ;B'       microbial phosphatase logistic parameter
.06 ;C'       microbial phosphatase logistic parameter
1.5 ;A1'      soil phosphatase exponential parameter
-1 ;B1'       soil phosphatase exponential parameter
.01 ;STABZ'   stabilization of microbial metabolites into c5
.75 ;WFPS'    percent water filled pore space, control on decomp
1 ;F4CN3'     CN3 factor ratio for N3TON4
1 ;F5CN3'     CN3 factor ratio for N3TON5
.5 ;F4CP3'    CP3 factor ratio for P3TOP4
1 ;F5CP3'     CP3 factor ratio for P3TOP5
```